



PHD

**Plovers, invertebrates and invasive predators: aspects of the ecology of some island populations**

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**PLOVERS, INVERTEBRATES AND INVASIVE PREDATORS:  
ASPECTS OF THE ECOLOGY OF SOME ISLAND POPULATIONS**

James Jack Harry St Clair

A thesis submitted for the degree of Doctor of Philosophy

University of Bath  
Department of Biology and Biochemistry

July 2010

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## Summary

This thesis makes progress in two broad fields of research, descriptive ornithology and invasion ecology, based largely on fieldwork in the Falkland Islands. Populations of two little-studied South American waders, the Two-banded Plover *Charadrius falklandicus* and the Rufous-chested Dotterel *Charadrius modestus*, were monitored over a four-year period at a single island site: in chapters two, three and four this thesis presents information on the diel pattern of incubation sharing by males and females of both species (the two species showed opposite diel sex-roles), data on morphology including sexual dimorphism (male-biased in both species), breeding systems data including estimates of mate fidelity, and for Two-banded Plovers, demographic estimates including annual survival rates of adults and hatching success of nests. These are among the first detailed studies of the breeding behaviour and life-histories of any southern South American waders. Concurrent with the single-site wader study, an inter-island natural experimental approach was used to investigate the effects of non-native mammalian predators, firstly on the expression of anti-predator behaviour in the Two-banded Plover (chapter five) and secondly on the relative abundance of populations of an endemic insect, the Falkland Camel Cricket *Parudenus falklandicus* (chapter six). The latter chapters both infer strong effects of non-native mammalian predators: firstly, Two-banded Plovers expressed much larger flushing distances in response to an approaching (human) stimulus at sites where feral cats *Felis catus* were present, although flushing distances were shorter when background exposure to humans was relatively high (I interpret these effects as generalisation and habituation respectively). Secondly, the relative abundance of Camel Crickets in a given habitat type was substantially higher in the absence of Norway Rats *Rattus norvegicus*, regardless of whether the rats were naturally absent or had been deliberately eradicated. Following the apparently strong effect of rats on insects in the Falkland Islands, in chapter seven I use literature from other island groups to review the effects of invasive rodents on island invertebrate populations; I conclude that negative effects are widespread and non-randomly distributed among invertebrate species, with large invertebrates particularly susceptible to rodent impacts. Finally, in chapter eight, potentially productive areas for future research and synthesis are suggested.

## **CHAPTER 1: INTRODUCTION**

James J. H. St Clair

## Overview

My objectives during this PhD fall into two categories: first, investigation of the life-histories and breeding systems of two species of wader in the Falkland Islands; and second, investigation of the effects of invasive mammalian predators on island populations.

Accordingly, the first three data chapters of this thesis describe aspects of the breeding systems and life-histories of two little-studied waders, the Two-banded Plover *Charadrius falklandicus* and Rufous-chested Dotterel *Charadrius modestus*, recorded at a single-island study site in the Falkland Islands. Specifically, chapters two and three describe the sharing of incubation and other aspects of the behaviour of (respectively) breeding Rufous-chested Dotterels and Two-banded Plovers, and chapter four describes additional aspects of Two-banded Plover behaviour and life-history, including estimates of survival rates for nests and adults.

The next two chapters (five and six) use a natural experiment paradigm to investigate some of the consequences of mammalian predator invasions for island populations. Chapter five is pitched at the level of individual behaviour, addressing the consequences of the presence/absence of a novel predator guild (mammalian predators including cats *Felis catus*) on the expression of anti-predator behaviour in island-breeding populations of the Two-banded Plover. Chapter six takes a population-level approach, using the natural experiment of rat *Rattus norvegicus* introductions to some of the Falkland's 750-odd islands to investigate the effects of rats on an endemic invertebrate genus, the Falklands Camel Cricket *Parudenus falklandicus*. Finally, in chapter seven I review of the evidence for rodent-invertebrate interactions on islands around the world.

## Why study avian life-histories and breeding systems? (Chapters 2-4)

More is known about the ecology and biology of birds than about any similarly-sized clade. This wealth of knowledge has ensured that the conservation status of the world's birds is better known than for any other group, and has also made birds a *de facto* model system for investigating ecological and evolutionary questions in a comparative framework (Baillie et al., 2004; Bennett and Owens, 2002).

Given the unparalleled body of knowledge that already exists about birds, how might further descriptive studies be justified? I suggest three inter-related reasons. Firstly, even though we know more about birds than other taxa, a great deal of variation remains to be described. As an example, the reproductive parameters of almost a quarter of the world's plover and sandpiper species remain entirely unstudied (Piersma et al., 1997; Table 1). Secondly, additional studies are worthwhile precisely *because* the ecology and biology of birds is better-described than any other class of organisms - in other words, the existence of a comparative context increases the face value of each new datum. Thirdly, further descriptive studies can be of value by addressing biases in existing avian datasets. A glance through any bird handbook shows that the representation of each data type is strongly associated with the time and effort required to collect it – thus 'easy' data such as clutch sizes and morphological measurements are available

for a majority of species, while 'difficult' data such as estimates of survival rates or nest attentiveness are available only for a minority (e.g. Cramp et al., 1985). A similar differential acts across geographical areas – for example, more data are available for species with distributions in Europe or North America than for those occurring in Africa or South America (del Hoyo et al., 1996; e.g. Piersma et al., 1997; Table 1), and island species are generally less well-studied than those on continents – as Cody (1971) stated, 'We have little information on the reproductive parameters of island birds other than clutch size'; this remains true for most island species today. Possibly correlated with this island effect, there is some evidence from the wader clade that species with small population sizes tend to be the least-studied (Thomas et al., 2003).

Geographical area	Number of species	Population size	Demography	Reproduction	Migration	Food & foraging	Overall score
Europe	36	28%	33%	0%	0%	8%	14%
North America	34	38%	71%	9%	0%	3%	24%
Australia & Oceania	16	0%	63%	19%	25%	25%	26%
Asia	35	51%	86%	34%	31%	49%	50%
Africa	19	95%	89%	21%	37%	58%	60%
South America	15	87%	100%	73%	53%	87%	80%
Overall	155	46%	70%	23%	22%	32%	39%

**Table 1:** *Lack of knowledge* (% of species about which nothing is known) for the plover (Charadriidae) and sandpiper (Scolopacidae) families according to data category and principal geographical region. Note that South America scores worst in almost all categories. Adapted with permission from Piersma et al. (1997)

Studies which seek to fill gaps and reduce bias in avian datasets are important for both evolutionary biology and conservation. On the one hand, conservation actions often depend on available data to assess extinction risk, prioritise conservation actions, and to model the population-level consequences of environmental scenarios such as habitat loss, harvesting or climate change (Cardillo et al., 2006; Mace et al., 2008). On the other hand, evolutionary biologists use the avian model in comparative analyses, and patchy, biased datasets hinder progress by restricting the hypotheses that can be tested, by limiting statistical control over potentially confounding variables, and by reducing the statistical power to detect relationships. A group of questions that is frequently addressed using comparative analyses of avian datasets concerns the evolution of breeding systems – patterns of mate choice, pair-bonding and parental care (Bennett and Owens, 2002).

The waders, a sub-group within the bird infra-order Charadriiides – to which the Two-banded Plover and Rufous-chested Dotterel belong – show a particularly diverse spectrum of breeding systems, ranging from monogamous species with biparental care to polygynous and polyandrous species in which the majority of parental care is conducted by (respectively) the female or the male (Reynolds and Székely, 1997). This unusual diversity, combined with a better knowledge of their ecologies, life-histories and phylogenetic relationships than of many other groups, means that waders are an excellent model system with which to investigate the ecological and intrinsic correlates of different breeding systems (Reynolds and Székely, 1997; Thomas et al., 2007). These analyses have become increasingly complex, using phylogeny to control for variation attributable to relatedness between species, path analyses to infer sequences in the evolution of co-occurring traits, and incorporating large datasets of inter-correlated phenotypic and environmental variables. The evolution of breeding systems is of interest to evolutionary biologists for a number of reasons: for one, the evolution of characteristics such as parental care is not fully understood and can appear paradoxical; and for another, breeding systems are vital components of animal life-histories, being associated with key parameters such as survival and recruitment, and potentially influencing – and being influenced by – effective population size and population processes (Bessa-Gomes et al., 2003; Liker and Székely, 2005; Saether et al., 2004; Saether et al., 1996). The study of variation in breeding systems can thus provide a route to understanding both social behaviour and population trajectories.

### **Why study invasive species? (Chapters 5-7)**

Invasive species, defined as those species that spread outside their natural range and have undesirable effects, are a major problem. Their economic impact can be substantial, and their effects on native species, with which they do not share a recent evolutionary history, can be catastrophic (Pimentel et al., 2000). Invasive species can cause populations of other species to decline by direct or indirect effects on mortality, reproduction, or traits that influence these parameters. It is a key goal of conservation scientists to understand the effects of invasives on other species, as such an understanding is clearly necessary to make informed decisions about the allocation of conservation effort, and the consequences of intervention or of inaction (Brooke et al., 2007; Caut et al., 2009; Zavaleta et al., 2001).

Ultimately, this understanding should help to avoid or avert species extinctions, which are not only undesirable in themselves but which can also have knock-on effects on many other species and thence on the emergent properties of ecosystems (Sekercioglu, 2006; Terborgh et al., 2001; White et al., 2006). Furthermore, although infrequently acknowledged, effects less extreme than extinction – such as the suppression of a previously abundant group – can have comparable effects on ecosystem properties, and additional effects including accelerated evolution (Davis, 2009; Gaston, 2008; Jackson et al., 2001; Prentis et al., 2008).

These complex interactions point to another reason to study species invasions – as a model with which to address more general questions in ecology and evolution (Blackburn, 2008; Sax et al., 2007). This utility is made possible by the recent or contemporary nature of many species invasions and eradications, which ensures that the resulting ecological and evolutionary processes can be observed directly. Additionally, species invasions are often incomplete and have occurred with a strong element of chance, meaning that they often produce relatively robust natural experiments in which characteristics of invaded ecosystems can be compared with those that remain uninvaded or from which the invasive has been deliberately cleared.

### **The Falkland Islands**

The Falkland Islands comprise two large islands (West and East Falkland) and over 750 smaller islands or islets, located approximately 500 km east of southern South America at latitudes from 51 to 53 degrees South. Geological evidence suggests that, like New Zealand, the islands originated as a fragment of Gondwana, the southern supercontinent that disintegrated in the Jurassic initiating the formation of today's southern hemisphere continents (Stone and Aldiss, 2000). Although the rocks indicate a close affinity with latter-day South Africa, the biota of the islands is essentially South American, having reached the islands either by dispersal over the sea or by some long-submerged land bridge (McDowall, 2005; Morrone and Posadas, 2005).

Despite the broad continental distribution of most of the birds of the Falkland Islands, a great deal of basic information is lacking for most of them. Most of the native birds of the Falklands have diverged little from their continental source populations. Only two, the flightless Steamer Duck *Tachyeres brachypterus* and weakly-flying Cobb's Wren *Troglodytes cobbi*, are considered to be fully speciated from their source populations, with divergence between the Falkland Islands and continental populations of other species probably limited by the recent or incomplete nature of their separation. In keeping with this interpretation, comparison of insular and continental DNA sequences from Two-banded Plovers and several songbird species show differences consistent with slight bottlenecking, but not with full isolation over long periods (Küpper, Campagna and St Clair, unpublished data).

Gene flow among strongly-flying groups including many birds is probably facilitated by the strong westerly winds that prevail in the latitudes of Patagonia, Tierra del Fuego and the Falkland Islands. The dispersive power of these winds (the 'roaring forties' and 'furious fifties') is evidenced by the arrival of vagrant bird species on the Islands after periods of strong wind (Pettingill, 1974; Woods, 1975). However, the ability of flightless animals to disperse on the wind is often limited, and the flightless animals of the Falklands are thought to have a high degree of endemism, with up to 70% of described insect species (which are largely flightless or weakly-flying) not known to occur on the continent (Fuller, 1996).

In common with many islands, the biota of the Falkland Islands is remarkably species-poor – for example, the islands boast only nine native species of passerine bird, five species of breeding wader and fewer than 300 described insect species. However, this depauperate community is

starting to increase dramatically through anthropogenic introductions, which already include the House Sparrow *Passer domesticus*, dozens of insect and plant species, and several mammals; in fact, since the extinction of the endemic Falklands Wolf *Dusicyon australis* in 1876 the only terrestrial mammals found in the islands have been anthropogenic introductions (Woods and Woods, 1997). These include those introduced deliberately, including sheep, reindeer, guanaco, cattle, horses, domestic cats and foxes – and those introduced incidentally or by accident, including rats *Rattus norvegicus* and *Rattus rattus* and mice *Mus musculus*. The effects of these introductions on the native biota have received relatively little attention; for example, it was only recently realised that Cobb's Wren is restricted in its distribution to islands free of mammalian predators, and that most other passerines are also negatively associated with the presence of rats (Hall et al., 2002; Woods, 1993). In fact, despite their global importance for many breeding bird populations, and their substantial contribution to the biodiversity of the United Kingdom, very little research has been carried out in the Falkland Islands on the effects of introduced predators (Croxall et al., 1984; Hilton and Cuthbert, 2010). Even so, the fragmented nature of the archipelago, coupled with the fact that invasive mammals occur on some islands but not others, means that the Falklands form a natural experiment that is ideally suited for investigating the effects of invasive mammals. To date, this opportunity has seldom been used to good advantage (for a notable exception, see Hall et al., 2002).

### **Island study systems**

Islands such as the Falklands make attractive study systems for several reasons. Perhaps the most prosaic is the ease with which island populations can be studied compared to mainland populations. Small, geographically constrained populations allow for more complete sampling (e.g. Griffith et al., 1999). Dispersal is often reduced, so it is easier to record detailed histories within and across generations (e.g. Grant and Grant, 1996). Island populations often occur at unusually high densities, meaning study organisms can be found more quickly than at continental sites (Blondel et al., 1988). Additionally, island populations often exhibit a reduction of anti-predator behaviour, and consequently individuals can be more easily captured or observed at close quarters without taking fright (Darwin, 1845). Of course, all of these advantages come with the caveat that they result from ecological differences between insular and continental habitats, and caution should be exercised when generalising between insular and continental patterns and processes.

A second attractive feature of island groups is their utility as natural experiments, whereby the effects of a variable of interest can be inferred by comparing islands that differ with respect to that variable. The approach has considerable value because the scale of natural experiments, set at the level of landscapes and populations, often exceeds the logistical limits of field experimentation (Diamond, 1986). For example, although of immense value in community ecology, experimental species removals and additions are usually expensive and (often) ethically proscribed, while natural variation is freely accessible. A further advantage arises from the fact that island communities are often depauperate, making them ideal systems for the



study of species interactions, as relationships between species pairs are likely to be simpler and stronger than in more complex (continental) communities (Jones, 2004; Vitousek, 2002; Woods and Woods, 1997). Island groups have long been used as natural experiments to investigate fundamental questions in ecology, such as species-area relationships, the role of competition and predation in structuring communities, and even the evolutionary consequences of such interactions (MacArthur and Wilson, 1967; Schluter et al., 1985; Schoener and Toft, 1983; Stone and Roberts, 1990).

A third interesting feature of islands is that insular organisms often show consistent morphological, life-history and behavioural differences from their continental relatives. For example, birds have frequently lost the ability to fly on islands and many island taxa show shifts in body-size; life-history characteristics such as offspring number, adult survival and mating systems often differ between island and continental populations; and island populations often exhibit ecological naïveté, the absence of traits found in continental populations such as an appropriate behavioural response to continental predators (Blondel, 2000; Darwin, 1845; Griffith, 2000; McCall et al., 1998). These differences are thought to result from consistent differences between the selective landscapes on islands and those on continents (MacArthur and Wilson, 1967; Scott et al., 2003), but remain poorly understood.

Finally, many of the characteristics that make populations of insular organisms straightforward and interesting to study (ecological naïveté, limited ranges and small population sizes) very likely contribute to a strongly elevated risk of extinction. Recent extinctions have probably occurred largely on islands, despite islands (the size of Greenland or smaller) constituting only 7% of the planet's land area (Millennium Ecosystems Assessment 2005). To take three examples, 88% of known bird extinctions, 68% of known mollusc extinctions and 84% of known terrestrial arthropod extinctions have occurred on islands (Baillie et al., 2004; Gillespie and Roderick, 2002). The status of island groups as hotspots of endemism and extinction, combined with their utility as natural experiments, makes them especially valuable to conservation scientists wishing to understand the consequences to biodiversity of perturbations such as species invasions, and of conservation interventions such as eradication and control (Sax et al., 2007; Towns, 2009).

The features of island study systems listed above are all relevant to the chapters that follow. The studies of life-history and breeding behaviour benefitted from the compact, dense and site-faithful populations of Two-banded Plovers and Rufous-chested Dotterels at a single site in the Falkland Islands. The studies of the effects of invasive mammalian predators relied on the natural experiment resulting from incomplete invasion of the archipelago by cats and rats. The massively elevated risk of extinction among island populations provided the motivation for much of the research presented here. And finally the potential differences between insular and continental populations and communities, while not explicitly investigated, should always be borne in mind when interpreting the results.

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**Chapter 2:      SEX ROLES OF THE RUFOUS-CHESTED DOTTEREL *CHARADRIUS*  
*MODESTUS* IN THE FALKLAND ISLANDS**

James J. H. St Clair, Clemens Küpper, Philipp Herrmann, Robin W. Woods and Tamás Székely

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JSC:    Fieldwork, Data Analysis, Writing (70%)  
CK:     Labwork, Writing, Comments (10%)  
PH:     Fieldwork, Data Entry, Comments (10%)  
RW:     Comments (5%)  
TS:     Comments (5%)

## ABSTRACT

Waders (sandpipers, plovers and allies) exhibit a greater diversity of breeding systems than any comparable avian taxon. However, our understanding of this diversity is hampered by the lack of basic information on the breeding systems of many species, particularly those with southern hemisphere (particularly South American) distributions. We investigated the breeding ecology of the Rufous-chested Dotterel *Charadrius modestus* in the Falkland Islands over four breeding seasons, to describe its breeding system for the first time and to test whether (like the congeneric and morphologically similar Eurasian Dotterel *C. morinellus*) the species exhibits sex-role reversal. Molecular and phenotypic sexing confirmed that females are neither brighter nor larger than males. Nests were biparental, and round-the-clock video monitoring of ten nests showed that males incubated during the day and females incubated at night, a reversal of the pattern found in other *Charadrius* species. Despite this unusual temporal pattern, the amount of time spent incubating by males and females at each nest was remarkably even. In summary, we reject the hypothesis of sex-role reversal in this population.

## INTRODUCTION

Waders have emerged as a valuable model system in the study of sexual selection and the evolution of parental care, largely because the clade exhibits great variation in breeding systems and phylogenetic relationships within the clade are relatively well resolved (Olson et al., 2009; Owens and Bennett, 1997; Reynolds and Székely, 1997; Thomas et al., 2007; Thomas et al., 2004). Although this variation is the focus of considerable research effort, existing knowledge of wader breeding systems is far from comprehensive and for many species, including the majority of those in South America, the breeding system remains entirely undescribed (Piersma et al., 1997).

The objectives of the current study were to describe for the first time parts of the breeding system of the Rufous-chested Dotterel *Charadrius modestus*, a South American endemic plover, and to test whether, like the morphologically similar Eurasian Dotterel *Charadrius morinellus*, the former species exhibits sex-role reversal. In sex-role reversed species (henceforth, SRR species) females tend to be larger and more ornamented than males, polyandry is common, and male-biased incubation and parental care are the norm (Bennett and Owens, 2002; Clutton-Brock and Vincent, 1991; Ligon, 1999; Oring et al., 1994). Although the evolution of sex-role reversal in parental care is not yet understood, it is likely that changes in the ornamentation of the sexes occur secondarily and reflect a change in which sex is subject to greater sexual selection: relatively more ornamented females are therefore diagnostic of sex-role reversal in a species. The identification and study of SRR species is of particular interest because they are exceptions to the common pattern of sex-role evolution, and thus provide a useful model for developing and testing theories of sexual selection (Andersson, 2005; Kokko and Jennions, 2008; Kokko et al., 2006).

The Rufous-chested Dotterel is a common breeding wader in the Falkland Islands and southern parts of South America, although basic information about its breeding system and other life-history traits is lacking (del Hoyo et al., 1996). The global population is estimated at between 133,000 and 1,063,000 individuals (Delany and Scott, 2006). Although population trends remain to be quantified, point counts at wintering sites suggest that the population may be in decline (Isaach and Martinez, 2003).

## METHODS

Fieldwork was conducted on the Falkland Islands, where the Rufous-chested Dotterel population is estimated at between 11,000 and 21,000 pairs (Woods and Woods, 1997). The study site was on Sea Lion Island, which has an area of approximately 905 hectares in an isolated location at the south of the Falkland Islands archipelago (52° 26' 0" S, 59° 5' 0" W). On Sea Lion Island, the study area was rectangular with an area of 165 hectares (1.5km x 1.1km) largely covered by oceanic Diddle-dee *Empetrum rubrum* heathland. The study was conducted during four consecutive Austral breeding seasons: from 25th October to 4th November 2005,



15th October 2006 to 10th January 2007, 13th October 2007 to 8th January 2008, and 20th September 2008 to 1st January 2009.

### **Field methods**

Nest searching was done either on foot or from a car. Nests were found by flushing the incubating parent and searching for the eggs, or flushing the incubating parent and watching it from a distance as it returned to its eggs. Nest locations were recorded using a handheld GPS receiver.

Adults were captured using a walk-in wire funnel trap placed over the eggs. Captures were made only after the third day of incubation, to reduce the probability of nest desertion (e.g. Kilpi et al., 2001). Adults were marked with a metal (Incoloy) ring on the right tarsus, and a unique combination of three darvic colour rings, a single colour ring being placed on the left tarsus and the two tibiae respectively. A small blood sample (25 – 50µl) was taken from the ulnar vein, and stored in Queen's lysis buffer (Seutin et al., 1991) for subsequent molecular sexing. Morphological measurements (body mass, and length of tarsus, bill and wing) were taken from all captured individuals following Székely et al. (2008). Adults were scored during processing as 'Bright', 'Dull' or 'Intermediate', based on the relative brightness of the plumage and definition between plumage areas, particularly the black chest band, rufous breast, white brow stripe and grey cap. Adults were never deliberately recaptured to avoid unnecessary stress. However, on four occasions birds which had been trapped in a previous year were unintentionally recaptured, and in each case they were ascribed to the same plumage category as they had been in the previous year, demonstrating that plumage assessment was repeatable.

Where possible both parents were identified at each nest (n = 80 out of 193 nests). This allowed estimates of divorce rate, defined (e.g. by Choudhury, 1995) as at least one partner re-pairing with another individual whilst both partners are still alive. It also allowed us to estimate Inter-Nest Distance (IND), defined as the distance between one nest and the following nest at which a marked individual or pair were identified. Finally, we also estimated the distance of nests from their nearest concurrent neighbour.

To determine sex-roles in incubation, motion-sensitive camera systems were placed at a sample of 10 nests during the 2008/2009 season (Bolton et al., 2007). The systems consisted of an Infra-Red LED array and a small digital camera with a neutral-density filter mounted on a short (~50cm) pole. Attached to the camera was a datalogger for recording the images, and a power supply (12v sealed lead-acid battery). Cameras were installed at nests in which one parent had been colour-ringed and one remained unringed, because the presence or absence of rings was used to identify the attending parent on the images. The datalogger and power supply were buried away from the nest-scraps, whereas the camera itself was installed from 50 to 100cm from the nest scrape, at a height of 15 to 30cm. Images were stored on 256MB SD-type data cards, which were changed approximately every eight hours.

In order to quantify the per-day contribution of each sex to incubation, nests which did not provide at least 24h of footage uninterrupted by technical problems were excluded. These uninterrupted multiples of 24h were used in order to give fair estimates of per-day attendance by each sex. Three nests were excluded by this criterion, leaving seven nests: one with a 24h period, five with a 48h period and one with a 72h period. Per-day of contribution of each sex at a given nest was calculated as the total time of all incubation bouts by the parent of that sex divided by the number of 24h periods.

To determine the proportion of day-time and night-time incubation carried out at each nest by the male and female respectively, male and female attendance was re-calculated separately for the periods of daylight (sunrise to sunset) and darkness (sunset to sunrise).

### **Molecular Sexing**

To determine sex-roles, 60 samples of adults from the 2005/2006 and 2006/2007 breeding season were molecularly sexed. DNA was extracted using an ammonium acetate method (Nicholls et al., 2000). We used [FAM] or [NED]-labelled P2/P8 primers (Griffiths et al., 1998) to amplify parts of the CHD fragment that are located on the Z and W chromosomes. Fragments on Z and W chromosomes differ in size, which results in sex-specific genotypes: males are usually the homogametic sex whilst females are heterogametic (but see Dawson et al., 2001; Griffiths et al., 1998; Küpper et al., 2009; Lee et al., 2002). CHD fragments were amplified with 10 µl polymerase chain reactions (PCRs). Each PCR contained approximately 10 ng of DNA and 0.25 units of Taq DNA polymerase (Bioline) in the manufacturer's buffer with a concentration of 0.5 µM of each primer, 2.0 µM MgCl<sub>2</sub> and 0.20 mM of each dNTP. PCR were run using a thermal cycler (MJ Research model PTC DNA engine) and the following program: one cycle of 3 min at 94°C followed by 35 cycles at 94°C for 30 s, 56°C for 30 s, 72°C for 30 s and a final extension cycle of 10 min at 72°C.

PCR products labelled with different dyes were post-PCR multiplexed (combining one NED and one FAM labelled sample each) and diluted. A fraction of the PCR product was loaded onto an ABI 3730 Analyzer using dye set DS-30, filter set D and ROX size standard for allele size determination, and the resulting genotypes were scored using GENEMAPPER 3.7 software (Applied Biosystems). We also estimated error rates for pairs in which both mates were caught and sampled (n = 15), by checking whether the molecular sexing resulted in assignment of exactly one male and female per pair.

### **Statistical analysis**

Statistical analyses were conducted using MINITAB 15 statistical software. Two-sample or paired *t*-tests were used when data conformed to assumptions of parametric testing;

nonparametric tests were used when these assumptions were violated. Summary statistics are presented as means  $\pm$  standard deviation, or medians when appropriate.

## RESULTS

### Molecular sexing and morphometrics

For 60 (95%) breeding adults molecular sexing produced a ZZ or ZW genotype whereas two cases failed to amplify and one sample apparently had a WW genotype. Males and females showed different genotypes according to fluorescent dyes. 17 samples that had been amplified with FAM labelled primers were homozygous for a 381 bp allele and classified as males (ZZ), whereas 17 samples were heterozygous, exhibiting a 381 bp and a 383 bp allele, and classified as females (ZW). 13 samples that had been amplified with NED labelled primers were homozygous for a 375 bp allele and classified as males (ZZ), whereas 11 samples were heterozygous exhibiting a 375 bp and a 381 bp allele and classified as females (ZW). The apparent error rate in a control group of 30 adults (15 breeding pairs) was 0%, since both the male and female were assigned unambiguously according to their CHD profiles. This included one pair in which both individuals were scored as 'bright' in the field.

Breeding adult females tended to have duller plumage than males; 26 (93%) females were classified as having 'dull' plumage, and 27 (84%) males were classified as having 'bright' plumage. Plumage brightness therefore correctly predicted sex in 88% of cases, and led to individuals being attributed the wrong sex in only 5% of cases. The remaining 7% represents 4 individuals which were recorded as having 'intermediate' coloration.

Among molecularly sexed adults ( $n = 60$ ) there was no significant difference between the males and females in body mass, tarsus length, wing length or bill length, although males were marginally larger in all measurements except bill length (Table 1; t-tests, all  $P > 0.09$ ).

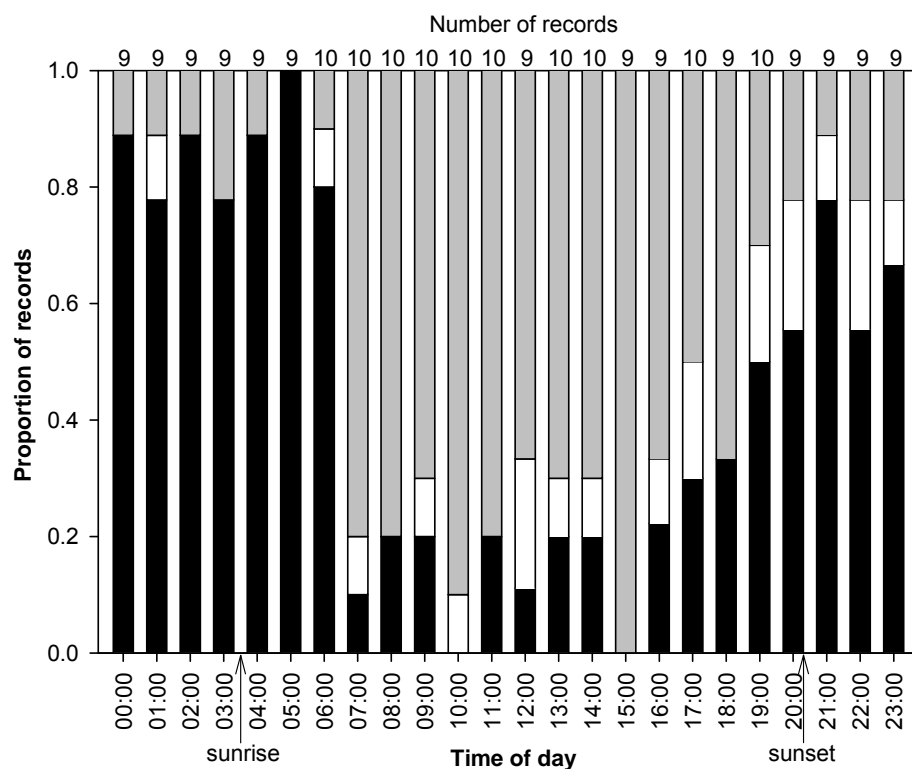
	Male (mean $\pm$ SD (n))	Female (mean $\pm$ SD (n))	t	P
Mass (g)	83.38 $\pm$ 4.51 (32)	83.14 $\pm$ 5.57 (27)	0.18	0.857
Wing length (mm)	154.40 $\pm$ 2.65 (30)	154.31 $\pm$ 4.27 (26)	0.10	0.922
Tarsus length (mm)	36.33 $\pm$ 1.23 (32)	36.07 $\pm$ 1.52 (28)	0.73	0.470
Bill length (mm)	19.17 $\pm$ 0.90 (32)	19.77 $\pm$ 1.11 (28)	1.32	0.090

**Table 1:** Morphometric data for molecularly sexed adults ( $n = 60$ )

### Incubation

Uniparental incubation did not occur, nests were never associated with more than two adults ( $n = 80$  nests at which two adults were colour-ringed), and there were no recorded instances of one individual being simultaneously associated with more than one nest. Seven nests (of ten

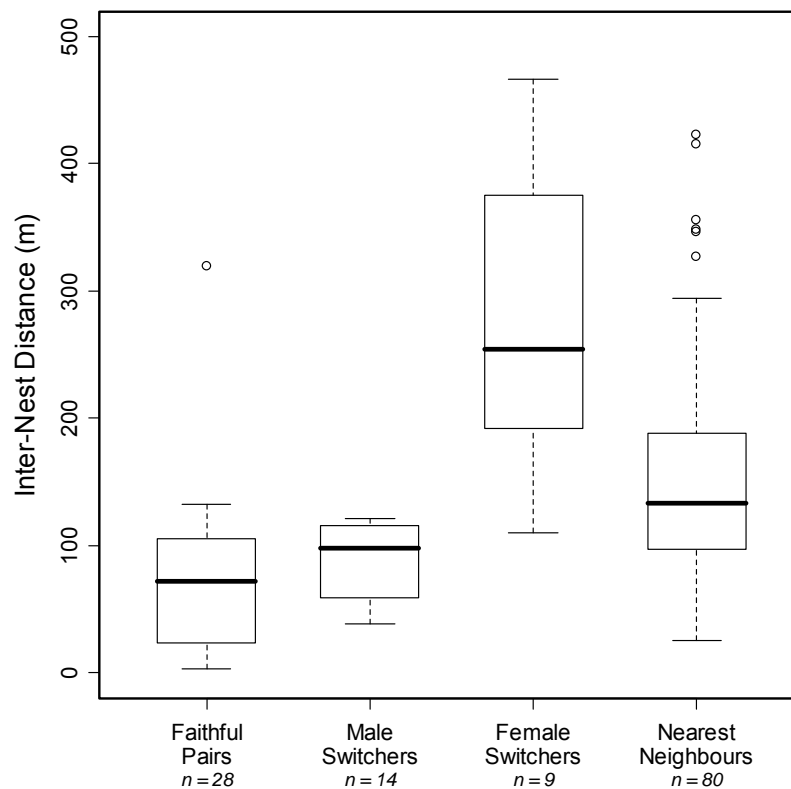
filmed) were used for analysis of incubation sharing as they contained full 24h periods uninterrupted by technical problems. Total nest attendance was high, and was shared approximately evenly between the sexes: males contributed  $11.4 \pm 2.7$  hours per day and females contributed  $11.5 \pm 2.3$  hours per day ( $n = 7$  nests). There was no significant difference in the proportion of incubation contributed per 24h between males and females (male minus female contribution, paired t-test,  $t = 0.05$ ,  $P = 0.961$ ,  $n = 7$  nests), although within periods of daylight or darkness the contributions of the sexes were different: males contributed  $63 \pm 14\%$  of incubation during daylight (versus 37% by females; paired t-test,  $t = 2.37$ ,  $P = 0.056$ ,  $n = 7$  nests) and only  $12 \pm 25\%$  of incubation during darkness (versus 88% by females; paired t-test,  $t = 4.08$ ,  $P = 0.007$ ,  $n = 7$  nests; Figure 1).



**Figure 1:** Diel incubation pattern in Rufous-chested Dotterels *C. modestus*. The proportion of female (black), male (grey) or no attendance (white) is given. One record was taken, on the hour, from each nest ( $n = 10$  nests). For nests that were filmed for more than 24h a record was selected at random for each period. Median sunrise and sunset times are marked by arrows.

### Nest site fidelity and territoriality

After nest failure, pairs re-nested close to their original nest later in the season (median 82m,  $n = 15$  pairs). This was not statistically different from the between-year Inter-Nest Distance (IND) of faithful pairs (median 25m,  $n = 13$  pairs, Mann-Whitney test,  $W = 159.0$ ,  $P = 0.182$ ). We thus pooled the data for within- and between-season INDs for subsequent analysis (overall median 72m,  $n = 28$  pairs). Like faithful pairs, males that changed mates between nesting attempts also moved short distances (median 98 m,  $n = 14$  males) although females that switched mates moved significantly further away (median 255 m,  $n = 9$  females: Kruskal-Wallis test,  $H = 19.3$ ,  $P < 0.0005$ , d.f. = 2; Figure 2). The median Nearest-Neighbour Distance for contemporary nests was 133m ( $n = 80$  nests).



**Figure 2:** Boxplot of distance moved (m) between successive nesting attempts by faithful pairs, and by males and females that switched mates between nesting attempts (not shown is an outlier among 'Female Switchers' at 865 m). The right-hand plot shows the nearest-neighbour distances of contemporary nests.

### Divorce/mate fidelity

Of 25 pairs in which both partners were known to be alive in the following year, 15 remained faithful and 10 (40%) divorced between years. Divorces within breeding seasons were rare: of

17 recorded instances of within-year reneating in which both individuals were colour-ringed, 16 pairs remained together and only 1 pair divorced (6%). The pair that divorced did so after their eggs hatched, but as the chicks were never seen it is likely they were predated before the female switched mates. The original male remained on his territory, and was not seen with a new female or nest.

## **DISCUSSION**

### **Molecular sexing and morphometrics**

The use of molecular markers has allowed us to identify individual Rufous-chested Dotterel individuals as either male or female, and to validate a method of sexing individuals in the field using a simple assessment of plumage brightness. It is likely that this method of sexing Rufous-chested Dotterels in the field can be improved upon using standardised methods such as colour charts (reviewed by Tucker et al., 1991) to assess plumage colour and brightness.

In SRR species, including the Eurasian Dotterel, females are typically larger than males, have brighter plumage, or both (Kálás, 1988; Owens et al., 1994; Székely et al., 2000). In contrast, our results demonstrate that female Rufous-chested Dotterels are not larger than the males and that their plumage is appreciably less bright. These findings suggest that in this species sexual selection for increased body size does not act more strongly on females than males, and that selection for brighter plumage acts more strongly on males than on females, which is consistent with the usual sex roles of monogamous species, in which it is the males which compete most intensely for resources (including access to mates) than vice-versa.

### **Nest site fidelity and territoriality**

Consistent with male competition for resources, breeding territories in the Rufous-chested Dotterel are apparently controlled by the males, as it is males (and faithful couples) that tend to move very short distances between successive nesting attempts whereas divorced or widowed females move much greater distances, to different territories. The same pattern has been recorded in White-fronted Plover *C. marginatus*, Semipalmated Plover *C. semipalmatus* and Piping Plover *C. melodus*, all typically monogamous plovers with biparental care (but see Amirault et al., 2004; Flynn et al., 1999; Haig and Oring, 1988; Lloyd, 2008).

### **Parental care**

Incubation in the Rufous-chested Dotterel is biparental, with each parent in a pair contributing an approximately equal amount of time to nest attendance. This contrasts strongly with the pattern in SRR species, in which the female contribution to incubation is typically much lower than that of the male. In the Eurasian Dotterel, females usually undertake little or no incubation

of their first clutch, although they may contribute partially to the incubation of later clutches (Kålås and Byrkjedal, 1984). Of 114 Eurasian Dotterel nests observed during one study, female incubation was observed at only seven (Nethersole-Thompson, 1973).

The incubation schedule, in which males incubate largely during the day and females incubate largely at night, has not to our knowledge been described before in any *Charadrius* species, although the pattern does occur among other genera such as the tundra plovers *Pluvialis* spp. (Byrkjedal and Thomson, 1998). Various hypotheses have been proposed to explain this variation in sex-specific diel patterns in incubation, such as a tendency for one sex to assume the majority of territorial defence during the day, the existence of energetic debt incurred by females during egg production which might favour off-bouts during the periods of maximum prey abundance, and selection imposed (on eggs or adults) by time-of-day dependent sex-biases in predation risk, whereby the least conspicuous sex would be expected to incubate during the day when visual predators are hunting (Skutch, 1957). The latter hypothesis is unlikely to be true in the Rufous-chested Dotterel as it is the brighter males that incubate during the day, and without detailed data on the energetic costs and benefits of egg production, territorial behaviour, anti-predator defence, and daylight versus nighttime incubation and feeding patterns, we can only speculate about the selection pressures that might lead to the observed temporal pattern of incubation.

However it may arise, the expression of a sex-bias in day/night incubation schedules may influence (or conceivably, be influenced by) the evolution of social and genetic breeding systems, as individuals of one sex will have more opportunities to form new pair bonds or copulate with new partners while their original partner is constrained by the incubation schedule (Ligon, 1999; Wallander, 2003). The reversed incubation pattern in the Rufous-chested Dotterel suggests that there may be a greater potential for the evolution of a polyandrous mating system than in other *Charadrius* species.

Parental care of chicks was not quantified in this study, as due to the vegetation structure and the crouching habit of chicks, it was difficult to determine the relative locations of chicks and parents without excessive disturbance. However, both parents tend to remain associated with the nesting territory until the chicks fledge, strongly suggesting biparental care of juveniles.

### **Divorce/mate fidelity**

At 40%, between-year divorce was common in the Rufous-chested Dotterel, and similar to rates recorded in other *Charadrius* species (for a summary, see Lloyd, 2008). We also observed a single instance of within-year divorce which arguably represents a case of serial polyandry. In fact, switching mates within a breeding season after a breeding failure is not unusual in plovers with 'normal' sex-roles; the within-year mate switching rate in *C. melodus* and *C. bicinctus* have been recorded at 34.6% and 20% respectively (Haig and Oring, 1988; Pierce, 1989).

## Conclusions and future directions

The sex-roles observed in the studied population of Rufous-chested Dotterel on Sea Lion Island in the Falkland Islands do not deviate from the 'normal' system of monogamy and biparental care, and we reject the hypothesis of sex-role reversal. However, these results should not be assumed to be representative of the species as a whole without investigation of other populations, because social behavioural traits such as mating system and parental care have been shown to vary considerably between populations of the same species. For example, in the Eurasian Dotterel the degree of polyandry and even sexual size dimorphism varies between populations and within populations through time (Kålås, 1988; Kålås and Byrkjedal, 1984; Nethersole-Thompson, 1973; Owens et al., 1994), and similarly in the Sanderling *Calidris alba* patterns of mate desertion and parental care are thought to vary both between and within populations (Parmelee and Payne, 1973; Pienkowski and Green, 1976). Such variation has been attributed to environmental differences which change the fitness costs and benefits of monogamy and biparental care relative to polyandry and male-biased parental care (Owens and Thompson, 1994; Székely et al., 2007). In the Falkland Islands, a harsh climate characterised by severe wind (Pettingill, 1960), low energy availability (Chown et al., 2005), and high densities of conspecifics and avian predators such as Skuas and Caracaras (Woods and Woods, 1997) may all select for prolonged and intensive biparental care and thus monogamy. However, because these environmental conditions will vary in different parts of the Rufous-chested Dotterel's range, we suggest the need to study populations at other sites including mainland South America.

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**Chapter 3: FEMALE-BIASED INCUBATION AND STRONG DIEL SEX-ROLES IN THE  
TWO-BANDED PLOVER *CHARADRIUS FALKLANDICUS***

James J. H. St Clair, Philipp Herrmann, Robin W. Woods and Tamás Székely

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JSC: Fieldwork, Data Analysis, Writing (75%)

PH: Fieldwork, Data Entry, Comments (15%)

RW: Comments (5%)

TS: Comments (5%)

## Female-biased incubation and strong diel sex-roles in the Two-banded Plover *Charadrius falklandicus*

James J. H. St Clair · Philipp Herrmann ·  
Robin W. Woods · Tamás Székely

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**Abstract** The relative contributions of males and females to incubation, and the diel schedules by which incubation is shared, are important breeding system traits. We used infra-red sensitive cameras to record incubation patterns at 13 nests of the Two-banded Plover *Charadrius falklandicus* in the Falkland Islands during both day and night. Because predation risk can affect incubation behaviour, we also recorded the diel pattern of nest predation in the wider study population. We found high nest attendance, female-biased incubation, and strong diel sex-roles, with females incubating during the day and males at night. We also found that incubation intermissions tended to be short but frequent, and were correlated strongly with the diel pattern of nest predations which occurred exclusively in the daylight hours (probably due to the absence of terrestrial mammals from the study site). Our results suggest that sex-roles are unusually strict in the Two-banded Plover, and that these strict sex-roles lead to inequality in incubation sharing and the level of exposure to sources of energetic cost such as disturbance by nest predators.

**Keywords** Incubation · Nest camera · Nest predation · Nocturnal · Sex-role · Temperature data-loggers

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J. J. H. St Clair (✉) · P. Herrmann · T. Székely  
Department of Biology and Biochemistry, University of Bath,  
Claverton Down, Bath BA2 7AY, UK  
e-mail: jjhsc20@bath.ac.uk

R. W. Woods  
68 Aller Park Road, Newton Abbot, Devon TQ12 4NQ, UK

### Introduction

Shorebirds (sandpipers, plovers and allies) exhibit a wide spectrum of sex-roles in incubation, with some species showing uniparental (female-only or male-only) incubation and a majority of species in which both the male and female always contribute (Reynolds and Székely 1997). It is increasingly realised that incubation is a highly demanding component of parental care, being both energetically expensive and risky (Amat and Masero 2004; Reid et al. 2002). It is thus a prime candidate for sexual conflict, the divergent interests of males and females over reproduction (Chapman et al. 2003): by transferring the burden of incubation to its partner, an individual could increase the time and energy available for breeding attempts with other partners and potentially increase its fitness (Brunton 1988; Kosztolányi et al. 2009). Variation in the relative contributions of males and females to incubation can thus be a sensitive indicator of sexual conflict and an important trait with respect to natural and sexual selection; as Trivers (1972) noted, heritable variations in parental investment can have major evolutionary consequences. However, the relative contributions of males and females have only been recorded in a small proportion of biparentally incubating bird species (Wallander 2003; Whittingham and Dunn 2001).

Studies of parental care in wild populations often seek to investigate patterns including the relative contributions of males and females to care based on data collected exclusively in the daylight hours (e.g. Bergstrom 1986). While the approach may be acceptable for mainly diurnal behaviours such as the provisioning of young by diurnal altricial birds, it can lead to biased estimates of parental roles whenever the sexes have a tendency to divide care according to a diel schedule. Methods which account for



parental activity during both the day and the night are therefore preferable; such methods include the use of infra-red cameras (Thibault and McNeil 1995), passive transponders (Kosztolányi and Székely 2002) and triangulation of radio transmitters (Warnock and Oring 1996).

We present nest-camera data on diel patterns in incubation in the Two-banded Plover *Charadrius falklandicus*, a small biparentally-incubating shorebird (body mass 70 g) that is widely distributed in the southern Neotropical region (del Hoyo et al. 1996). We investigated this species in the Falkland Islands, where it is abundant (Woods and Woods 1997). We quantify the relative contributions of males and females to incubation, determine whether incubation is shared according to a diel schedule, and explore patterns in nest attentiveness over the course of the day. Because nest predation risk has the potential to explain much of the variation in incubation patterns (Ghalambor and Martin 2002), we also recorded the diel distribution of nest predations in the wider study population using temperature data-loggers (Hartman and Oring 2006).

## Methods

### Fieldwork

Field data were collected between October and December 2008 on Sea Lion Island at the south of the Falkland Islands archipelago in the South Atlantic (52°26'0"S, 59°5'0"W); the island has an area of 905 ha, and lacks mammalian nest predators such as cats, foxes and rats. Two-banded Plover nests were located by searching suitable habitat on foot within the study area. Motion-sensitive cameras were then used to monitor incubation routines at 13 nests at which at least one parent had been captured, sexed and colour-ringed, allowing the sexes to be distinguished. Two-banded Plovers can be reliably sexed in the field, as males typically have stronger black breast-bands and a rich chestnut plumage on the nape (Woods 1988). The camera systems are composed of an Infra-Red LED array and Infra-Red sensitive digital camera mounted on a short pole, and a data-logger and power supply which were buried up to 4 m from the nest scrape (Bolton et al. 2007). A software trigger was used to record a series of images whenever movement occurred in the centre of the camera's frame (i.e. whenever the sitting bird moved its head, shifted position on the eggs, or left or arrived at the nest). An average of 1,381 images were taken per hour of recording. The images were written to SD-type data cards with a unique electronic time stamp. The data cards were changed approximately every 10 h (mean  $\pm$  SD:  $10.3 \pm 1.8$  h,  $n = 13$  nests).

In the nest-camera images, individuals were identified by recording the presence or absence of colour rings on

both the outgoing and incoming bird. Additionally, differences between individual males and females in the width and completeness of the upper breast-band allowed identifications to be confirmed while the birds were incubating.

Temperature data-loggers were installed at 50 further nests using methods described by Hartman and Oring (2006) to record the diel timing of nest-predation events. Briefly, a temperature data-logger was buried in the centre of each nest-scrape, under approximately 5 mm of lining material; a control data-logger was similarly buried approximately 30 cm from the nest scrape. Of the 50 nests, 27 predation events were recorded and the time of predation was clearly discernable (from a rapid decrease to ambient temperature) in 24 of these.

### Data analysis

To compare the relative contributions of males and females over the full day using nest-camera images, 24 on-the-hour images—one for each hour, from 00:00 to 23:00 hours—were taken from each nest, recording the presence of 'male', 'female' or 'neither'. Because some records on a given day were often missing (for example, due to a lack of camera memory) or potentially compromised (for example, due to an observer visit to the nest during the preceding hour) the 24 on-the-hour records were sampled randomly from the remaining 'good' records across all recorded days for that nest. If a nest lacked a record for a particular hour on every day of recording, the nest was excluded from this analysis (leaving  $n = 8$  nests in total). For each nest, the number of records (of 24) contributed by the male and female were then expressed as a proportion; male and female per-day contributions were compared by subtracting male from female proportions, and testing for a difference from zero (paired  $t$  test). Nests which provided fewer than 24 on-the-hour records were *not* excluded from the graph of diel sex-roles because the graph shows the pattern of nest attendance in the population, and not within individual nests.

A 'shift' was considered as the period from the time a parent settled on the eggs to the time it left to be replaced by its partner. Change-over times (when one partner replaced the other) were also recorded. Because birds often took breaks (henceforth 'intermissions') from incubation during their shift, incubation was broken up into shorter periods (henceforth 'bouts'). For each nest, the median durations of bouts and intermissions were recorded separately for males and females. Shifts, bouts and intermissions were excluded from analysis if they were compromised by observer activity (for example, the bouts preceding and following observer visits to the nest were excluded).

Rates of intermission in incubation were estimated by counting the number of intermissions (excluding observer-



caused intermissions and change-overs between the sexes) that occurred in each 2-h period during the day. Linear quadratic regressions were used to test the relationships between time-of-day and predation events, and time-of-day and frequency of intermissions in incubation; for the latter test, a single (mean) frequency of intermission was calculated for each time period. Finally, we tested for correlation between the response variables (nest predation events and mean frequency of intermission).

Data are presented as mean values  $\pm 1$  standard deviation when normally distributed, and differences between males and females were analysed using paired *t* tests. Intermission and bout durations and change-over times were not normally distributed and are thus presented as median values with inter-quartile range (1st to 3rd quartile, in parentheses), and analysed using Mann–Whitney *U* tests. To avoid pseudoreplication, when more than one datum was recorded for a given individual, nest or time-period, an average was calculated for analysis.

## Results

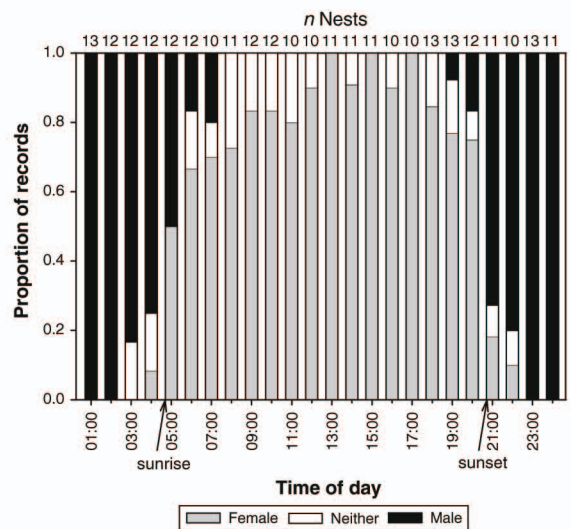
### Diel patterns of incubation

Incubation was biparental, with males tending to incubate at night and females tending to incubate during the day, and change-overs between the sexes occurring around sunrise and sunset (Fig. 1); female shifts started at a median of 69.0 min after sunrise (1.4–119.0 min,  $n = 12$  nest medians), and male shifts started at a median of 15.0 min before sunset (64.4 to  $-2.5$  min,  $n = 13$  nest medians).

Including only those nests for which attendance was recorded at least once for every hour of the day ( $n = 8$ ), total nest attendance was 92%, and males were on the nest for a significantly lower proportion of records than females both over a full 24 h and during the daylight hours only, although they attended the nest on the majority (85%) of the hours of darkness (Table 1).

Consistent with the period of daylight exceeding the dark period, female incubation shifts were significantly longer than those of males, although there was no significant difference between the sexes in the duration of intermissions or bouts of incubation (Table 2).

Change-overs between the sexes were quick, lasting a median of 0.1 min (0.1–0.2 min,  $n = 5$  nest medians). Observer-caused intermissions were relatively infrequent, occurring only when data cards were exchanged (2–3 per day). The parents returned quickly to the nest following these visits: from the moment the observer walked away from the nest to the return of the incubating parent took a median 1.7 min (1.0–3.4 min,  $n = 13$  nest medians).



**Fig. 1** Diel sex-roles in nest attendance in the Two-banded Plovers *Charadrius falklandicus* in the Falkland Islands. On-the-hour nest attendance records (male, female or neither) were sampled from nest camera footage of 13 nests (maximum one record per nest per hour) and expressed as a proportion of the total number of records for each hour. Median sunrise occurred at 04:43 hours and sunset at 20:52 hours

‘Natural’ intermissions in incubation were frequent and varied over the course of the day, with a low rate of intermission at night increasing to a peak rate of intermission during the middle of the day (Fig. 2); time-of-day was thus a powerful predictor of intermission rate [ $F_{2,9} = 19.69$ ,  $P = 0.001$ ,  $r^2 = 0.81$ ,  $n = 12$  (mean) intermission rates].

### Diel pattern of nest predation

We recorded the exact times of 24 nest predation events in our study population; these events followed a diurnal pattern, with no events occurring during the hours of darkness and a peak during daylight hours (Fig. 2); thus, time-of-day accounted for most of the variation in nest predation frequency ( $F_{2,9} = 10.23$ ,  $P = 0.005$ ,  $r^2 = 0.70$ ,  $n = 12$ ). Intermission rate and nest predation frequency followed the same diel pattern, and were thus highly correlated (Pearson correlation,  $r^2 = 0.68$ ,  $P = 0.014$ ,  $n = 12$ ).

## Discussion

The diel sex-roles in incubation are apparently stronger in the Two-banded Plover than in most other *Charadrius* species (Wallander 2003), with males attending the nest for almost all of the night and females for almost all of the day (Table 1; Fig. 1). The pattern of female incubation during



**Table 1** Incubation sharing by Two-banded Plover *Charadrius falklandicus* pairs in the Falkland Islands

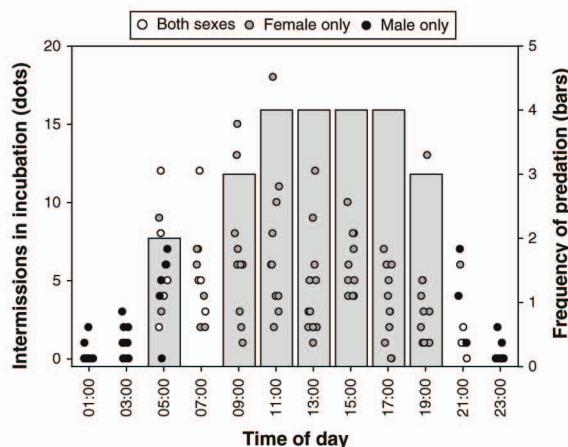
	Proportion of records (mean $\pm$ SD)			Sex comparison (paired <i>t</i> tests)		
	Male	Female	Neither	<i>n</i> nests	<i>t</i>	<i>P</i>
Full day	0.34 $\pm$ 0.08	0.58 $\pm$ 0.06	0.08 $\pm$ 0.04	8	4.83	0.002
Daytime only	0.06 $\pm$ 0.08	0.85 $\pm$ 0.09	0.09 $\pm$ 0.07	8	14.60	<0.001
Night-time only	0.85 $\pm$ 0.14	0.05 $\pm$ 0.07	0.09 $\pm$ 0.13	8	12.38	<0.001

Proportion of on-the-hour records for which nests was attended by the male, female or no bird, for full days (24 h), daytime only (05:00–20:00 hours inclusive) and night-time only (21:00–04:00 hours inclusive)

**Table 2** Average durations of incubation shifts, bouts and intermissions in the Two-banded Plover

	Duration $\pm$ SD or (q1–q3)		Sex comparison	
	Male	Female	<i>t</i> or <i>U</i> ( <i>n</i> pairs)	<i>P</i>
Shifts (hrs)	8.7 $\pm$ 1.7	15.0 $\pm$ 1.2	<i>t</i> = 7.92 (8)	<0.001
Bouts (mins)	19.5 (8.8–30.5)	10.5 (8.1–15.2)	<i>U</i> = 208 (13)	=0.108
Intermissions (mins)	1.0 (0.7–2.2)	1.3 (0.6–1.6)	<i>U</i> = 158 (13)	=0.383

Shifts were normally distributed (mean  $\pm$  1 SD.; paired *t* test). Bout and Intermission data were left-skewed and treated nonparametrically (median, interquartile range; Mann–Whitney *U* test)



**Fig. 2** Rate of intermission in the Two-banded Plover. Each point represents the number of intermissions at a single nest during a 2-h period; jitter is added for clarity. Change-overs and observer-caused intermissions are not counted here. Black symbols for male-only periods, grey symbols for female-only periods, and empty symbols for periods during which a change-over occurred (i.e. both sexes present). Bars show frequency of actual nest predations recorded by temperature data-loggers over the course of the study, in 2-h bins

the day and male incubation at night is consistent with other members of the genus (Wallander 2003), although the sympatric Rufous-chested Dotterel *Charadrius modestus* shows a reversal of this pattern (St Clair et al. 2010). A comparison among the biparentally incubating shorebirds demonstrates that the tendency for male incubation at night and female incubation during the day is not a rule: for

example, the tundra plovers (*Pluvialis* spp.) and several lapwings (*Vanellus* spp.) exhibit more female incubation during the night (Byrkjedal and Thomson 1998; Ward 1990). These patterns suggest that among closely related species the same diel sex-roles tend to prevail, indicating that the roles are often evolutionarily conserved. The other striking pattern is that diel sex-roles in incubation are apparently the norm, with weak or nonexistent diel sex-roles in biparental incubation seldom reported; weak diel sex-roles were reported for three sandpipers (*Calidris* spp.) by Norton (1972) and Pierce (1997) although their high-latitude study sites were in perpetual daylight.

Most explanations for diel sex-roles in incubation assume that incubation at different times of day has divergent costs and benefits that males and females are differently equipped to cope with. For example, the daylight-incubating sex may face greater risk from visual predators and be required to sit for more time (as daylight hours exceed night-time hours), whereas the night-time incubating sex must cope with a greater risk from olfactory predators, and possibly a higher energetic cost per unit of time (due to lower temperatures). Added to these factors, temporal variations in prey abundance and feeding opportunities may drastically change the costs of incubation during the day or night, as one sex is constrained to incubate while the other can feed freely. The relative magnitudes of these different costs and benefits, and their differential effects on male, female and offspring fitness, are still largely addressed speculatively rather than empirically.



We found that females experience higher rates of intermission in incubation than males, an effect that appears to be associated with time-of-day rather than sex-specific behaviour because male intermission rate increases through the course of the morning and decreases during the evening (Fig. 2). Our results also highlight a candidate mechanism for this difference in intermission rate: a strong diel pattern in nest predation risk which is highly correlated with frequency of incubation intermissions through the day. Because many factors besides predation risk vary according to diel patterns, it is not possible to distinguish causes from consequences in this case; for example, it may be that higher daytime temperatures allow females to leave the nest to feed, while the costs of doing so at night are prohibitive due to lower ambient temperatures. However, it seems probable that the frequent very short intermissions during the day are at least partly the result of anti-predator behaviour (flushing) in response to avian predators such as Striated Caracaras *Phalacrocorax australis*, which are abundant on Sea Lion Island (Woods and Woods 1997). There are likely to be costs associated with such frequent anti-predator behaviour, including increased energy expenditure (Biebach 1986) and chronically elevated levels of stress hormones such as corticosteroids (Clinchy et al. 2004); the lack of nocturnal nest predators (mammals) at our study site means that these potential costs are faced largely by the female. Furthermore, frequent intermissions are also likely to be costly to the developing embryo, potentially resulting in egg temperature fluctuations away from the developmental optimum, lower mean egg temperatures and consequently long incubation times (Martin et al. 2007; Olson et al. 2006). Consistent with the latter idea, Two-banded Plovers exhibit a remarkably long incubation period of 29.6 days (St Clair et al., in preparation).

Once specialised diel sex-roles in incubation arise, there are intriguing potential consequences for the evolution of breeding systems. For example, in biparental species, the adaptation of the sexes to particular incubation roles may be reinforced by positive feedback: adaptation promotes role specialisation and role specialisation favours adaptation. The resulting reinforced specialisation of sex-roles may strongly favour continued cooperation and biparental care (Barta et al., in preparation), as specialised parents may experience higher fitness than unspecialised 'jack-of-all-trades' parents through improved survival of themselves and their offspring. In turn, their specialisation may mean that they are unable to effectively assume the role of the other parent, ensuring that desertion by one parent severely reduces the success probability of the reproductive attempt. Such feedback adds a further dimension to the complexity of breeding system evolution, and it is increasingly realised that mate choice, mating systems and parental care are strongly interrelated (Alonzo 2010; Székely et al. 2000). If

specialisation in parental roles reaches a threshold level, it could represent a powerful selection pressure for social monogamy, and a mechanism for the contingent irreversibility (sensu Szathmáry and Maynard Smith 1995) of biparental cooperation.

A further possibility is that if diel sex-roles are 'hard-wired' in that change-over behaviours are triggered by changing light levels at dawn and dusk, latitudinal shifts in breeding range towards the poles (where hours of darkness are reduced) would lead to changes in the relative amounts of incubation contributed by males and females; this idea may be assessed in the Two-banded Plover by testing the prediction that incubation will be more evenly shared at lower latitudes in continental South America where there is greater parity between the hours of daylight and darkness. While biparental care may be most evolutionarily stable when day and night are not of very different lengths, changes in day-length would effectively reduce the time and energy available to partners of one sex for extra-pair courtship or polygamy, while increasing the variance in extra-pair possibilities for the other. In consequence, among taxa with an evolutionary history of strict diel sex-roles, we might expect a higher incidence of uniparental care at very high latitudes, a trend which has been shown to exist among shorebirds in general with respect to post-hatching care (García-Peña et al. 2009) but which has not yet been addressed with respect to care during incubation.

In summary, our findings show that Two-banded Plover pairs share incubation according to a diel schedule, and that males tend to incubate at night and females during the day. This diel schedule is associated with unequal sharing of incubation over 24 h (because day-length exceeds night-length, females spend more time at the nest) and with other inequalities, such as a higher rate of intermissions in incubation for females. The diel pattern of intermissions is consistent with frequent flushing during the day in response to elevated predation risk, although there are other possible causes such as the need to forage or express territorial behaviour. These patterns suggest several directions for future research, both into the proximate causes of variation in incubation behaviour (factors such as photoperiod and predation risk), and the potential interaction between sex-role specialisation and the evolution of breeding systems.

## Zusammenfassung

Die vornehmlich weibliche Bebrütung und stark tageszeitabhängigen Geschlechterrollen des Falklandregenpfeiffers *Charadrius falklandicus*

Die relative Beiträge von Männchen und Weibchen zur Bebrütung und der tägliche Rhythmus, in dem die



Bebrütungswechsel erfolgen, sind wichtige Merkmale von Fortpflanzungsstrategien. An Hand von Infrarotkameras wurden Bebrütungswechsel an 13 Nestern des Falklandregenpfeiffers *Charadrius falklandicus* auf den Falklandinseln bei Tag und Nacht aufgezeichnet. Weil Bedrohung durch Fressfeinde das Bebrütungsverhalten verändern kann, wurden außerdem tägliche Erscheinungsmuster von Nesträubern in der gesamten Studienpopulation erfasst. Wir beobachteten hohe Nestpräsenz, Bebrütung vermehrt durch das Weibchen und ausgeprägte, tageszeitabhängige Geschlechterrollen, wobei Weibchen tagsüber brüteten und Männchen nachts. Wir fanden eine starke Korrelation zwischen Bebrütungsaussetzern, die meist kurz waren, aber häufig vorkamen, und dem Auftreten von Nesträubern, die nur tagsüber erschienen (wahrscheinlich, weil am Studienort keine terrestrischen Säugetiere vorkamen). Unsere Ergebnisse legen nahe, dass Geschlechterrollen bei Falklandregenpfeifern ungewöhnlich genau festgelegt sind und dass diese strengen Geschlechterrollen zu einer Ungleichheit führen, sowohl in der Aufteilung der Bebrütung als auch in der Belastung durch Ereignisse mit hohen energetischen Kosten, wie die Beeinträchtigung durch Fressfeinde.

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**Chapter 4:      LIFE-HISTORY AND BREEDING BEHAVIOUR OF TWO-BANDED PLOVERS**  
***CHARADRIUS FALKLANDICUS* IN THE FALKLAND ISLANDS**

James J. H. St Clair, Philipp Herrmann, Robin W. Woods and Tamás Székely

Manuscript – note spelling is U.S. ‘English’

JSC:    Fieldwork, Data Analysis, Writing (80%)

PH:     Fieldwork, Comments (10%)

RW:     Fieldwork, Comments (5%)

TS:     Fieldwork, Comments (5%)

## **ABSTRACT**

The basic biology and ecology of South American shorebirds is relatively poorly described. Here we provide the results of the most detailed study to date on a breeding population of Two-banded Plovers *Charadrius falklandicus*. Fieldwork was conducted over four years at a study site in the Falkland Islands, and data on morphometry, demography and ecology of a breeding population are presented here for the first time. Our results indicate that the Two-banded Plover has a protracted nesting period, low nest survival and little recruitment into the breeding population, but that adults have high survival and are generally site-faithful and monogamous. We discuss the significance of these findings in terms of global life-history patterns and conservation.

## **Ecología de la reproducción de Chorlos Doble-collar (*Charadrius falklandicus*) en las Islas Malvinas**

### **RESUMEN**

La biología y ecología básica de las aves playeras sudamericanas está relativamente poco descrita. Aquí, presentamos resultados del estudio más detallado, a la fecha, sobre una población de Chorlos Doble-collar (*Charadrius falklandicus*) durante su reproducción. El trabajo de campo se realizó durante cuatro años en un sitio de estudio en las islas Malvinas, en donde se midió, por primera vez, su morfometría, demografía y ecología reproductiva. Nuestros resultados indican que el Chorlo Doble-collar tiene un periodo de nidificación prolongado, baja sobrevivencia de nidos, escaso reclutamiento en la población reproductiva, y los adultos tienen alta sobrevivencia, generalmente son fieles al sitio de reproducción y son socialmente monógamos. Discutimos sobre el significado de estos descubrimientos en términos de los patrones globales de las historias de vida y la conservación.

## INTRODUCTION

Less is known about the plovers and sandpipers of South America than those of any other region of the world (Piersma et al., 1997). The knowledge we lack about demographic rates, reproductive ecology, foraging requirements and migration behavior is potentially vital for the identification of species, habitats and areas of conservation concern (Owens and Bennett, 2000). These actions are increasingly necessary: of the shorebird species well-known enough to allow estimation of population trends, over half are in decline or already extinct, while only nine per cent are increasing (Delany and Scott, 2006). The data we currently lack are not solely of value to conservationists; birds – and shorebirds in particular – are increasingly used as a model system in comparative analyses of the evolution of breeding systems, parental care, migration and other life-history traits (Garcia-Peña et al., 2009; Olson et al., 2008; Owens, 2002; Székely and Reynolds, 1995; Thomas et al., 2007). Currently, such analyses are potentially biased because of a geographical skew in the distribution of available data (towards temperate-zone Northern hemisphere species), which results in general conclusions being drawn from a sample that is both spatially nonrandom and, because life-histories have been shown to vary latitudinally and between hemispheres, potentially unrepresentative of the global avifauna (Martin, 2004; Piersma et al., 1997). The gap in current knowledge about South American plovers is particularly incongruous given the evidence that the plover clade (family Charadriinae) has its evolutionary origins in South America (Joseph et al., 1999).

To improve, at least incrementally, the understanding of the ecology, behavior and demography of southern Neotropical shorebirds, we color-ringed and monitored a breeding population of the Two-banded Plover *Charadrius falklandicus* (Latham, 1790) at a single site in the Falkland Islands over four successive breeding seasons. To date, knowledge of the ecology of the Two-banded Plover has been limited to a handful of field-guide descriptions, a few localised studies of distribution, and some detailed studies of the foraging behavior of wintering individuals (Alfaro et al., 2007; D'Amico et al., 2004; Garcia-Peña et al., 2007; Woods, 1975). Questions such as the breeding phenology, breeding system, sexual size dimorphism, and survival rates of adults and young all remain neglected. This lack of knowledge is not due to rarity: globally, the Two-banded Plover population is bracketed as between 46,000 and 140,000 individuals (Delany and Scott, 2006) with the Falkland Islands population estimated at between 7,000 and 13,000 pairs (Woods and Woods, 1997). The species is locally abundant and widely distributed in the temperate Neotropical region, with a breeding range extending from approximately 37°S to 55°S, and with migrant individuals reaching as far North as Rio de Janeiro on the East coast of South America and Peru on the West (Woods and Woods, 1997; C. Küpper unpublished data).

The global conservation status is listed as Least Concern (IUCN, 2009) although the population trend for this species is unknown and there is some point-count evidence that the continental population is in decline (Luis Espinosa, personal communication). The migratory habits of this species remain undescribed in any detail, although at least part of the continental population migrates while the Falkland Islands population is probably sedentary (del Hoyo et al., 1996; Woods, 1975).

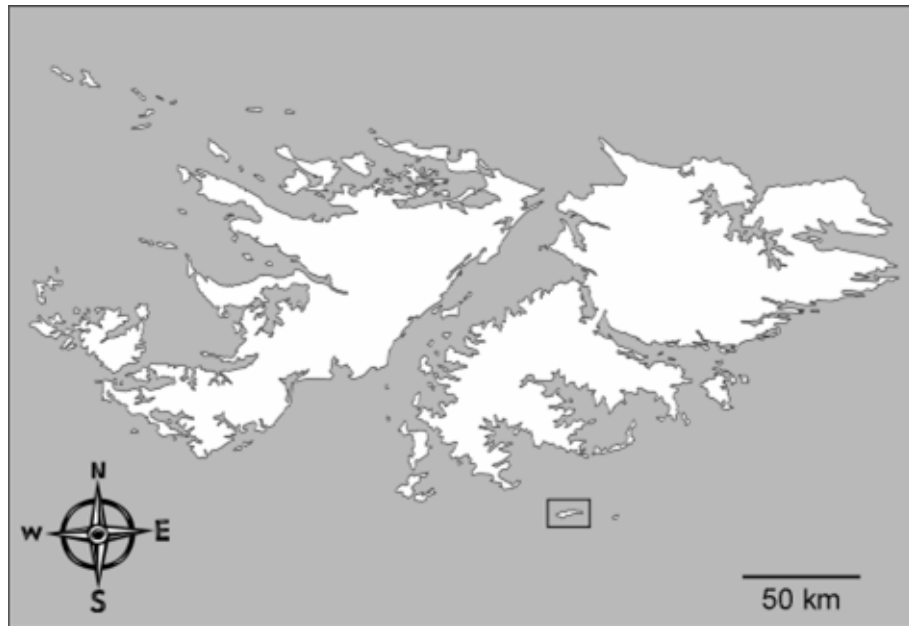
## METHODS

The study was conducted during four consecutive Austral breeding seasons, from 25 October to 4 November 2005, 15 October 2006 to 10 January 2007, 13 October 2007 to 8 January 2008, and from 20 September 2008 to 1 January 2009.

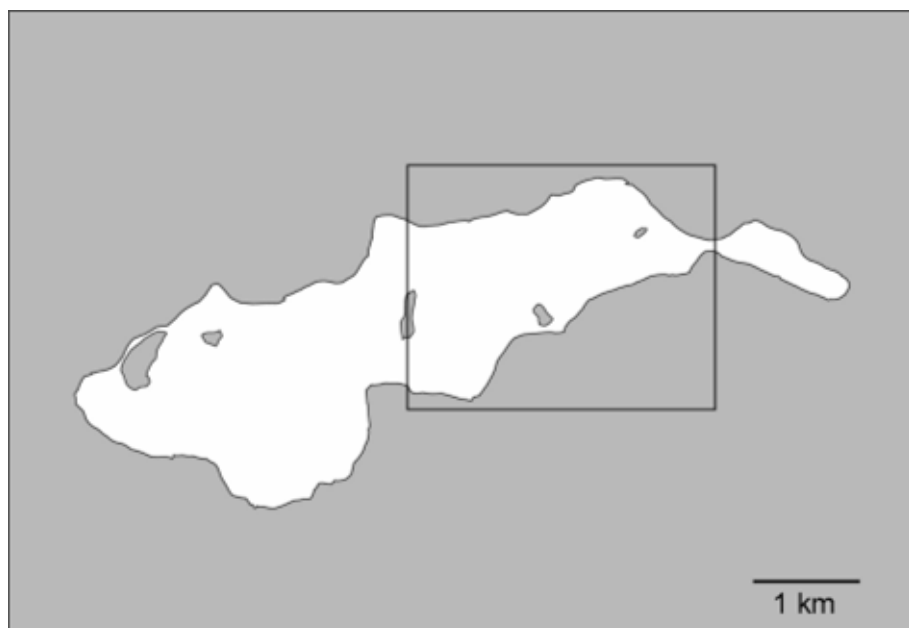
The study area was located on Sea Lion Island, which is approximately 905 hectares in an isolated position at the south of the Falkland Islands archipelago in the South Atlantic ( $52^{\circ} 26' 0''$  S,  $59^{\circ} 5' 0''$  W; Fig. 1a). On Sea Lion Island, the study area was approximately 300 hectares (Fig 1b) and contained various types of land cover including sand beaches, short turf, and heathland.

Field methods were adapted from those described by Székely et al. (2008). Nest-searching was usually conducted on foot, and nests were located by flushing the incubating parent and watching it back to its eggs or by scanning the ground for sitting birds. The UTM coordinates of each nest were recorded using a handheld GPS receiver. We estimated the stage of incubation using the floatation method, which was calibrated using nests of known age (Liebezeit et al., 2007). Only one egg from each clutch was floated in order to minimise time spent at the nest, and eggs were not floated during periods of inclement weather. Nests were monitored (median interval 2 days) until success or failure was recorded. When the exact date of the outcome was not known, it was estimated as the midpoint between the date of the first visit after the outcome and the date of the preceding visit (Mayfield, 1975).

Adults were trapped on the nest using a walk-in funnel trap once the eggs had been incubated for at least three days, as parents may be less likely to desert more developed clutches (e.g. Ackerman and Eadie, 2003). Similarly, to reduce stress to parents and developing embryos, trapping was not carried out during periods of precipitation or high winds. Morphometric measurements of captured individuals included wing length (to the nearest mm), tarsus length (to 0.02mm), bill length (to 0.02mm) and body mass to the nearest 0.5g. Adults were sexed according to the definition and brightness of their plumage; in males, the back of the head and nape of the neck are a rich chestnut color, while the female coloration is more muted (Woods, 1975). All captured birds were marked on the right tarsus with a unique metal (Incoloy) band, and in addition adults received a unique combination of three Darvic color-bands on the left tarsus and two tibiae respectively. Juvenile birds were given a single Darvic band on the left tarsus, avoiding the possibly conspicuous colors of red, orange and yellow. Opportunistic resightings of color-banded adults were recorded throughout the study to allow estimation of between-year adult survival rates.



**Figure 1a:** The Falkland Islands including Sea Lion Island



**Figure 1b:** Location of the study area on Sea Lion Island

## **Data Analysis**

The nest survival algorithm in Program MARK (Dinsmore et al., 2002; White and Burnham, 1999) was used to estimate the daily nest survival rate. Two models were specified: (1) a mean value of daily nest survival rate was estimated for the whole period of incubation, and (2) daily nest survival rate was allowed to vary according to the age of the nest. It was unnecessary to use Likelihood Ratio Tests for model selection because there was no competing model within two Akaike Information Criterion (AIC) units of the top model, and so the model with the lowest AIC was accepted (Burnham and Anderson, 2002).

Data on resightings of color-banded adults were used to estimate annual adult survival using a standard Cormack-Jolly-Seber approach in program MARK (Lebreton et al., 1992; White and Burnham, 1999). To minimise errors resulting from possible misreading of color-band combinations, individuals which were sighted fewer than three times in a season were excluded from the dataset. Using a recaptures-only algorithm, a maximal model for annual survival was specified in which the estimated probability ( $P$ ) of re-sighting an individual (given its presence) and estimated survival probability ( $\Phi$ ) were allowed to vary between years and between the sexes. A series of reduced models were then specified in which between-year and between-sex differences were constrained systematically while other parameters were allowed to vary, concluding with a minimal model with only two parameters, single estimates of both ( $P$ ) and ( $\Phi$ ) with no sex difference. Model selection was as described for nest survival.

Data were compared using  $t$ -tests when they satisfied the assumptions of parametric testing (proportion data were arcsine-transformed prior to analysis and body-mass data were square-root transformed to equalise variances), and Mann-Whitney tests when these assumptions were violated. Minitab version 15 statistical software was used for all comparison tests.

## **RESULTS**

### **Survival and Recruitment**

The minimal two-parameter model of annual adult survival estimated a single value each for recapture probability ( $P$ ) and survival probability ( $\Phi$ ) of marked adult individuals. Other candidate models, in which ( $\Phi$ ) and/or ( $P$ ) were allowed to vary between years, and/or different estimates were made for males and females, were not competitive according to AIC (Table 1) and so the minimal (two parameter) model was accepted. According to this model, the probability of re-sighting banded individuals given their presence in the population ( $P$ ) was very high at  $0.964 \pm 0.025$  (mean  $\pm$  1 s.e.), with annual adult survival for both sexes ( $\Phi$ ) estimated at  $0.922 \pm 0.024$ .



Model	$\Delta AIC$	Model Likelihood	$K$	Deviance
$\Phi(.)P(.)$	0	1.000	2	14.268
$\Phi(t)P(.)$	3.41	0.182	4	13.565
$\Phi(.)P(t)$	4.03	0.133	4	14.187
$\Phi(t)P(t)$	5.44	0.066	5	13.514
$\Phi(.sex)P(.sex)$	4.02	0.134	4	14.173
$\Phi(t.sex)P(t.sex)$	14.63	0.001	10	12.033

**Table 1:** Candidate models and model selection criteria for annual adult survival of Two-banded Plovers in the Falkland Islands across four years.  $K$  is the number of parameters. (t) signifies that the preceding parameter was allowed to vary between years; (.) signifies a single estimate for the study period. The AIC of the top (accepted) model was 197.54.

132 juveniles were banded over the first three years of the study. Recruitment into the breeding population was confirmed in nine instances in which birds that were banded as juveniles were subsequently captured while breeding. Seven of these were females, and two were males; as females were easier to capture due to their daylight incubation role (St Clair et al., 2010) this skew may reflect differences in capture success rather than a sex bias in juvenile dispersal. Five of the returning individuals bred in their first year. There was no evidence for within-site natal philopatry within the study area among these individuals, as offspring nests were located a median of 923m from their natal nest, which was not significantly different from the distance of 914m expected by chance given the distribution of nesting habitat (Mann-Whitney test,  $W = 10926$ ,  $n_1 = 9$  returning individuals,  $n_2 = 149$  random pairs of nests,  $P = 0.919$ ).

### Nesting Ecology and Nest Survival

In total, 294 Two-banded Plover nests were found over 4 seasons. Excluding 60 clutches which may have been incomplete (which were destroyed before incubation had begun, or before the age of the nest could be ascertained) 73% of 234 clutches contained three eggs and 26% contained two eggs. The remaining 1% contained either 1 or 4 eggs, leading to a population average of 2.74 eggs per clutch. There were no recorded instances of a pair raising two broods within a season, although pairs readily nested again after the loss of earlier clutches.

The inter-egg interval was estimated as  $2.8 \pm 0.5$  d ( $n = 16$  clutches, based on estimates of laying date for the second and third egg only). From the date nests were found with a single egg to the estimated date on which the third egg was laid averaged  $4.9 \pm 0.7$  d ( $n = 14$  clutches, based on discovery date of first egg and estimated lay date of the third egg).

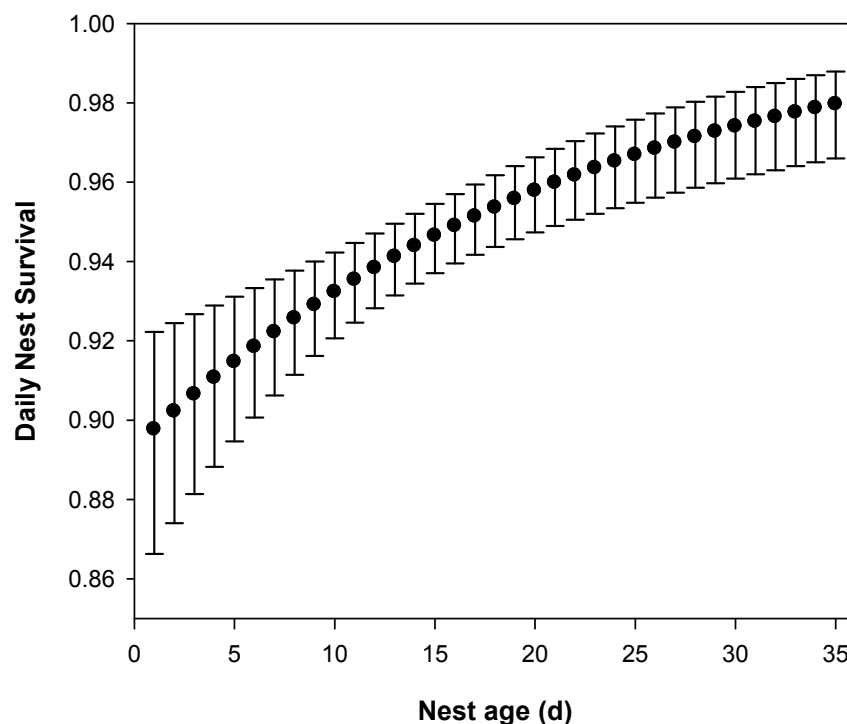
The duration of incubation (from the production of the final egg to hatching) was estimated as  $29.6 \pm 1.9$  days ( $n = 8$  successful clutches for which laying date of the final egg was known).

Of the 294 nests found, 81 hatched at least one chick, 180 failed and 33 had an unknown outcome.

The minimal model of nest survival, in which a single value of nest survival was estimated, did not compete according to AIC and the maximal (time-varying) model was thus accepted (Table 2). According to this model daily nest survival rate increased as a function of nest age, with as many as one in ten nests failing each day during their early stages (Figure 2). The mean value of daily nest survival was  $0.943 \pm 0.004$  (mean  $\pm$  s.e.); raised to the power of the 35-day age of successful nests, this predicts a per-nest probability of success of 12.8%.

Model	$\Delta$ AIC	Model Likelihood	$K$	Deviance
$\Phi(\text{age})$	0	1.000	2	917.58
$\Phi(.)$	19	0.000	1	938.58

**Table 2:** Candidate models and model selection criteria for nest survival of Two-banded Plovers in the Falkland Islands.  $K$  is the number of parameters. The AIC of the top (accepted) model was 921.58.



**Figure 2:** Daily survival rate of Two-banded Plover nests (mean values  $\pm$  95% confidence intervals)

Mammalian predators are absent from Sea Lion Island, although there is a wealth of potential avian predators of adults and/or nests and young, including Striated Caracara *Phalacrocorax australis* and Falkland Skua *Catharacta antarctica*. Trampling by larger birds such as penguins and sheldgeese may also be a significant cause of nest failure in this population; these large birds were often seen walking close to plover eggs, and seen to trample a nest in one case. 20 of the 180 failed nests showed signs of trampling such as crushed eggs, although as some trampled clutches would have been quickly scavenged the real figure is likely to be higher.

#### *Parental care and mate fidelity.*

Incubation was biparental, with no recorded instances of mate desertion during incubation, or of more than two birds attending the nest ( $n = 123$  nests at which both parents were color-banded). Post-hatching parental care was not quantified, but biparental care until fledging appeared to be usual.

Of 23 breeding pairs in which both partners were known to be alive in later years, 19 pairs nested together in the following year while in 4 pairs at least one partner was found to have switched mates, a estimated between-year divorce rate of 17%. In 19 within-year renesting attempts at which both parents were identified at both nests, 17 were by faithful pairs and two involved couples which had separated, an estimated within-year divorce rate of 11%. One of these couples had the only four-egg clutch encountered in the study, which was (unusually) abandoned; the female bred later in the year with a new male whereas her previous mate was observed alive but not apparently paired. In the other recorded divorce, chicks hatched successfully from the first nest but later in the year both parents were found renesting with different partners; the chicks were not seen subsequent to hatching and it is likely that they died before the parents divorced.

#### **Morphometrics**

Dimension	Females	Males	Sex-comparison t-test		
	Mean $\pm$ sd ( $n$ )	Mean $\pm$ sd ( $n$ )	$t$	d.f.	$P$
Mass (g)	69.83 $\pm$ 5.06 (84)	71.46 $\pm$ 4.12 (57)	2.02	139	0.045
Wing (mm)	130.61 $\pm$ 6.33 (83)	133.91 $\pm$ 2.46 (55)	3.68	136	< 0.001
Tarsus (mm)	28.47 $\pm$ 1.26 (84)	29.02 $\pm$ 1.13 (57)	2.66	139	0.009
Bill (mm)	17.31 $\pm$ 0.85 (85)	17.92 $\pm$ 0.63 (57)	4.61	140	< 0.001

**Table 3:** Morphometrics of Two-banded Plover adults

The population exhibited male-biased sexual size dimorphism, as males were significantly larger than females in all measurements (Table 3).

## DISCUSSION

The Two-banded Plover is one of several under-described South American plovers, and this study represents a substantial increase in our knowledge of its ecology on its breeding grounds. The picture that emerges from these data is one of a highly site-faithful, monogamous shorebird, exhibiting a high rate of annual survival, small clutch size, low offspring (nest) survival and low recruitment into the breeding population.

Across species, many of these traits have a tendency to co-occur within the same life history. For example, high adult survival and low recruitment are often associated: low recruitment caused by yearling dispersal or predation of nests and juveniles may relax competition among the adult age-classes, allowing greater longevity; alternatively, saturation of resources (such as breeding territories) by long-lived adults may effectively inhibit recruitment, possibly even selecting for juvenile dispersal (Bowler and Benton, 2005; Hatchwell and Komdeur, 2000). High adult survival is also often associated with high adult site fidelity, as when life expectancy is high the costs of adult dispersal should tend to increase relative to its benefits (Bowler and Benton, 2005). Finally, recent theoretical work suggests that high adult survival rates should also be associated with monogamy, because long-lived individuals have more opportunities to assess the cooperativeness of different partners and to maximise their fitness by pairing repeatedly with 'tried and tested' cooperative partners (McNamara et al., 2008).

Although there are notable exceptions, all of these life-history traits are commonly found together in shorebirds including the plovers. However, even among closely related species, annual adult survival in the Two-banded Plover appears particularly high: at 92% it exceeds the observed rates for all but one of the seven *Charadrius* species for which comparable data were collated by Lloyd (2008). Furthermore, if adult birds do disperse out of the study area, the value of 92% annual adult survival may well be an underestimate. The values for other traits such as site and mate fidelity are also high relative to other plovers (Lloyd, 2008). The existence of high adult survival and associated traits in this plover population is consistent with trends in the global distribution of life-history traits among birds: not only do species in the southern hemisphere tend to be longer-lived than their relatives in northern latitudes, but a similar trend is thought to prevail on islands relative to the adjacent continent (Blondel, 2000; Martin, 1996). Such differences are thought to be associated with large-scale trends in seasonality and/or predation, with low levels of both thought to prevail in the southern hemisphere and on islands (MacArthur and Wilson, 1967). It is notable that one species with life-history traits very similar to those of the Two-banded Plover in the Falklands is also an insular southern-hemisphere species, the New Zealand Dotterel *C. obscurus* (Marchant and Higgins, 1993).

However the ancestral environment might favour their evolution, such slow life-histories can leave populations vulnerable to decline when extrinsic factors such as exotic predator

introductions, emergent diseases, climate change, or destruction of migratory staging habitat, cause adult survival rates to decrease (Saether and Bakke, 2000). This suggests that the collection of basic demographic data of southern hemisphere shorebirds such as the Two-banded Plover, and the assessment and monitoring of their conservation status, should perhaps be pursued more diligently than is currently the case.

The observed increase in daily survival rate with nest age is a common phenomenon, and possibly results from relatively speedy predation of poorly-sited or otherwise vulnerable nests (Dinsmore et al., 2002). However, even among established nests, daily nest survival was remarkably low in the studied population. Low nesting success resulted from low daily survival combined with unusually long inter-egg intervals and incubation periods; a congeneric species, the Double-banded Plover *C. bicinctus*, takes approximately three days less from laying the last egg to hatching (Bomford 1988). The low daily nest survival rate probably results from intense predation pressure from several abundant nest predators. Sea Lion Island is unusual in that it has large breeding colonies of seals which support dense populations of gulls, skuas, caracaras and tussacbirds which all also prey on plover eggs. The reason for such a long nesting period is less clear, although it may be part of a slow life history strategy, whereby rapid reproduction is traded-off against adult survival (Roff, 1992). Alternatively (or additionally), long nesting periods may result from energetic constraints acting on the female during egg laying, and on both parents during incubation. The harsh weather of the Falkland Islands (particularly its strong winds) may substantially increase the rate at which adults and eggs lose heat, a potential source of energetic constraint (Hilton et al., 2004). Added to this, the sub-antarctic islands are thought to be 'low-energy' ecosystems, and it is possible that the amount of available energy limits incubation efficiency (Chown et al., 2005).

Of course, the characteristics of the observed Two-banded Plover population are not necessarily representative of other populations. The species has a broad breeding distribution including the southern third of continental South America and various island groups (such as the Falklands and Tierra del Fuego) and which spans a wide range of latitudes, from the southern tip of Chile to Brazil. From the variety of habitats, climates and biotas encompassed in this range, we would predict considerable intraspecific variation in morphological, behavioral and life-history traits, of which the described population should exhibit only a portion. Furthermore, the potential geographic barriers presented by the Andes mountains, and the 400 km stretch of the South Atlantic Ocean which separates the Falkland Islands from the continent, may also play a role in generating and maintaining intraspecific variation by restricting gene flow between populations. Consistent with the existence of a genetic bottleneck between continental South America and the Falkland Islands there are apparent morphological differences between populations, with the Falklands birds often exhibiting a weak or broken breast-band, in contrast to the strong, defined breast-band of the continental birds (Woods and Woods, 1997). We suggest the need for further studies on this species, both to explore the genetic and phenotypic variation that no doubt exists across its wide geographical range, and to address the many aspects of its ecology that remain poorly described. For example, knowledge of the migratory

status of different populations is sketchy at best, and the strategies and flyways of migrating individuals are under-researched (Piersma et al., 1997); population size is effectively unknown, with estimates of the continental population size spanning an order of magnitude (Delany and Scott, 2006); and vital aspects of demography, such as age composition, sex ratios and sources of juvenile and adult mortality remain to be explored.

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**Chapter 5:      INTRODUCED PREDATORS DECREASE TOLERANCE TO HUMAN  
DISTURBANCE IN A BREEDING SHOREBIRD**

James J. H. St Clair, Gabriel E. Garcia-Peña, Robin W. Woods & Tamás Székely

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## ABSTRACT

Non-lethal disturbance can impose fitness costs, particularly during sensitive life-history stages such as reproduction. Prey animals are thus expected to assess the costs and benefits of expressing anti-predator behaviour in different circumstances, and to respond optimally according to the perceived risk of predation. One prediction of this hypothesis is that the response to non-lethal disturbance should be elevated when the risk of predation is high, although few studies have tested this prediction with respect to the distribution of actual predators in nature. We used landscape-level variation in the distribution of large mammalian predators (feral cats) to investigate anti-predator behaviour in a small breeding shorebird, the Two-banded Plover *Charadrius falklandicus*. We used eight sites in the Falkland Islands and Argentina, and measured the flushing distances of incubating Two-banded Plovers in response to a controlled human approach to the nest. We found that flushing distances were increased at sites where mammalian predators were present, and decreased where exposure to humans was high. These results were additive, and we interpret them as the effects of generalisation and habituation respectively.

## INTRODUCTION

Human disturbance is increasingly a cause for conservation concern, particularly as development and recreational use of ecologically sensitive areas increases (Baudains and Lloyd, 2007; Boyle and Samson, 1985). Apparently harmless activity by humans can cause the expression of anti-predator behaviours such as fleeing or avoidance in many animals. This behaviour is thought to result from generalised responses to stimuli which might signal imminent predation risk. Such generalised responses should be particularly useful when prey animals have limited information available on which to base their decisions (Koops, 2004). However, this behaviour may carry costs in terms of energy expenditure and lost opportunities to feed or reproduce, which can potentially translate into reduced fitness (Creel and Christianson, 2008; Cresswell, 2008; Gill et al., 2001). Therefore, when prey animals have the opportunity and ability to assimilate information about predation risk under different circumstances, theory predicts that the information should be used to assess the risk of predation and respond optimally by trading the magnitude of the perceived risk against the costs of a given response (Lima and Dill, 1990; Ydenberg and Dill, 1986). A number of studies present results consistent with this hypothesis, associating the expression of anti-predator behaviour with its costs and benefits in terms of residual reproductive value, changes in energetic state, and factors affecting the risk of predation including prey condition, environmental state, characteristics of the stimulus, and prior experience of predation risk (reviewed in Lima and Dill, 1990; Montgomerie and Weatherhead, 1988; Stankowich and Blumstein, 2005).

The risk-disturbance hypothesis of Frid & Dill (2002) states that prey animals should assess their risk of predation (perceived risk) and use this information to modulate their response to approaching stimuli including humans. One of several predictions of the risk-disturbance hypothesis is that responses to human disturbance will be stronger when the risk of predation is high (Frid and Dill, 2002). However, perhaps because the background risk of predation is difficult to assess, relatively few studies have tested this prediction (Peters and Otis, 2005). Consistent with predator introduction affecting the perceived risk associated with humans, studies in reptiles have found that flight initiation distances in response to human approaches are substantially higher at island sites with introduced mammalian predators (cats) compared to those without, usually interpreted as a general increase in anti-predator behaviour under increased predation risk (Berger et al., 2007; Stone et al., 1994).

Here we investigate variation in flight initiation distance (henceforth 'flushing distance') of a small ground-nesting shorebird (the Two-banded Plover *Charadrius falklandicus*) in response to an approaching human, with respect to the presence or absence of mammalian predators and other variables including human activity and reproductive traits.

Flushing distances provide an excellent model with which to investigate risk perception in prey animals, because the costs and benefits of different behaviours vary with the distance between the prey and its potential predator. The expressed flushing distance should thus represent a solution to the trade-off between the perceived risk and the costs of reacting (Ydenberg and Dill,

1986). Consequently, for a given species, flushing distances are intimately associated with perceived risk of predation, and variations in flushing distance are frequently used to investigate perceived predation risk in different circumstances (e.g. Bonenfant and Kramer, 1996; Cooper, 2009; Rodriguez-Prieto et al., 2009). We focussed on two aspects of information use by breeding Two-banded Plovers. Firstly, we asked whether exposure to mammalian predators alters the perceived risk associated with human approaches to the nest; and secondly, we asked whether increased exposure to humans reduces the perceived risk associated with human approaches.

We investigated these two questions at the landscape level in the Falkland Islands and South America, using variation generated by the 'natural experiment' of mammalian predator introduction to the Falkland Islands. Following recent studies, we used spatial variation in predator distribution to investigate the behavioural impacts of predation risk on prey species (e.g. Berger et al., 2007; Blumstein and Daniel, 2002; Bonnet et al., 2005; Massaro et al., 2008; Peluc et al., 2008; Stone et al., 1994). Two-banded Plovers are widely distributed in southern South America including the Falkland Islands, and they are an excellent system for flushing distance studies because they nest on the ground in open habitat so that nests are easy to find and approach methodically, and they are distributed across sites with high variation in their exposure to predators. All islands in the Falklands have lacked native mammalian predators since the eradication of the Falklands wolf *Dusicyon australis* in 1876, while some islands now contain introduced mammalian predators including feral cats *Felis catus* and others remain free of them (Slater et al., 2009; Woods and Woods, 1997).

Globally, feral cats are major predators of island birds (Nogales et al., 2004), including small ground-nesting shorebirds and their eggs (Cohen et al., 2009; Dowding and Murphy, 2001; Keedwell and Sanders, 1999). For example, on the South Atlantic island of Saint Helena feral cats accounted for 67% (12/18) of remotely monitored nest predations of the St Helena Plover *Charadrius sanctahelenae* (FE Burns, unpublished data), and in New Zealand feral cats are major predators of adults, juveniles and nests of the Double-banded Plover *Charadrius bicinctus* (Dowding and Murphy, 2001); both of these species are closely related to the Two-banded Plover, and similar in size and habits. There are detrimental effects of feral cats on the Falkland Islands avifauna in general, including other small shorebirds (Woods and Woods, 1997). Although no studies exist on the interaction between feral cats and Two-banded Plovers, it is likely that cats represent a substantial predation risk to both adult plovers and their offspring.

## **METHODS**

### **Study organism**

The Two-banded Plover is a locally abundant but little-studied Neotropical shorebird with a body mass of approximately 70g (J St Clair et al. submitted). It is a ground-nesting precocial bird, nesting in open habitats with ground-hugging vegetation, and females conduct the majority of

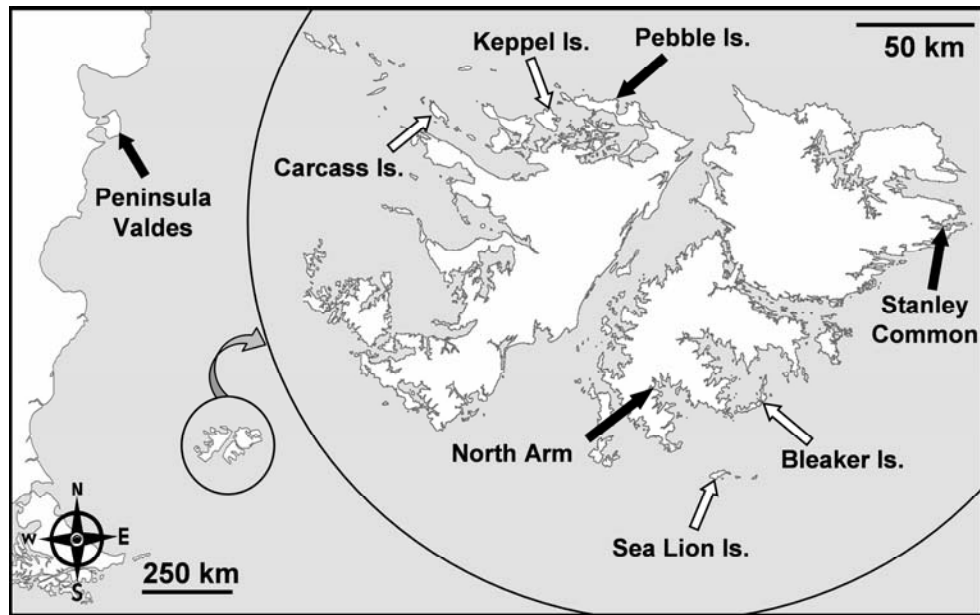
incubation during daylight (St Clair et al., 2010). During the day, the non-incubating (male) bird usually feeds or rests on beaches or feeding grounds away from the nest site (J St Clair et al, unpublished data). A clutch of 1-3 eggs (median 3) is laid in a shallow scrape in the ground, and hatches approximately 30 days after the clutch is completed (J St Clair et al. submitted). The Falkland Islands population appears to be largely resident (Woods, 1975), although unpublished genetic data implies some interbreeding between island and continental populations (J St Clair et al, unpublished data).

### **Field methods**

Fieldwork was conducted between 10th October and 8th December 2007 at eight sites; seven in the Falkland Islands archipelago and one at Península Valdés in continental South America. The Falkland Islands sites were located on six islands: East Falkland (North Arm in the South and Stanley Common in the North-east), Bleaker Island, Carcass Island, Keppel Island, Pebble Island and Sea Lion Island (Figure 1; Table 1). Most sites were visited for only a few days, and all nests found at these sites were included in the study. Two sites (Sea Lion Island and Península Valdés) were part of longer-term studies, and flushing distance data were collected only from nests at which the parents had not been previously captured. All Falkland Islands data were collected by the same observer, while a second observer collected data from Península Valdés (see data analysis section below).

### **Response variable**

Flushing distances were estimated by approaching a Two-banded Plover nest at a measured pace of approximately  $1 \text{ m s}^{-1}$ , from a start point of approximately 100m (Blumstein, 2003). As only one approach was made at each nest, sample sizes are equal to the number of nests. The starting direction was determined by natural obstacles, and the necessity of maintaining clear line-of-sight to the incubating female. When the incubating female flushed from her eggs, the distance from the approaching observer to the nest scrape was measured out using 1 m paces (Baudains and Lloyd, 2007). In a small number of cases ( $n = 3$  nests) the incubating bird was observed to flush as the observer neared the 100m starting position; as these points were potentially influential, it was decided *a priori* to include them in the dataset. Both observers ( $n = 2$ ) wore similar, muted clothing, and observations were carried out in dry weather during hours of full daylight (earliest 6:30h, latest 20:00).



**Figure 1:** Location of study sites, showing the continental study site at Península Valdés, the location of the Falkland Islands and (inset) detail of the Falkland Islands. Solid arrows show sites with mammalian predators, and open arrows sites without.

## Explanatory variables

### *Exposure to mammalian predators*

Sites were selected according to the presence or absence of introduced cats (Woods and Woods, 1997). At Península Valdés, two other mammalian predators were also present (domestic dog *Canis familiaris* and Argentine grey fox *Pseudalopex griseus*) although as none of the four cat-free sites in the Falkland Islands contained any of these predators, sites were categorised with respect to large mammalian predators as either 'present' or 'absent'.

### *Exposure to humans*

To investigate whether flushing distances were associated with the amount of exposure to humans at different sites, we estimated rank human activity levels (henceforth, 'human activity') at each site according to land use and estimates of the numbers of residents and recreational walkers. Sites varied from an uninhabited island at one extreme, through sites used to varying degrees for agriculture and tourism, to a beach on the outskirts of a medium-sized town (approximately 50,000 inhabitants) at the other. Human activity ranks were highly consistent between seven independent observers (mean adjusted  $r^2 = 94.6\%$ , all  $P < 0.001$ ). These observers were given description of each site on land use, numbers of residents and recreational users, and were asked to rank the sites with respect to human activity. Using GPS data we also recorded the distance (in m) of each nest from the nearest human habitation; this

measure (henceforth 'nest isolation') was used as a proxy for the level of human exposure for individual nests.

#### *Reproductive value*

The expression of anti-predator behaviour is thought to be associated with the reproductive value of the clutch, which should be higher in larger clutches and those which are closer to hatching (Lima, 2009). Hence, when a plover nest was found we recorded the date, time, and number of eggs, and the age of the nest was estimated using the egg-flotation method calibrated against nests of known age (Liebezeit et al., 2007). Because reproductive value can vary according to the time of the breeding season (Sackman et al. 2006), the Julian calendar date of each observation was included as a covariate. Clutches contained one, two or three eggs. Since only eight clutches contained only one egg, these were pooled with two-egg clutches into a clutch-size factor with two levels, '3 eggs' ( $n = 95$  nests) and '< 3 eggs' ( $n = 35$  nests).

Site Name	Mammalian Predators	Human activity	Julian sampling dates	<i>n</i> nests
Bleaker Island	absent	3	321 - 323	16
Carcass Island	absent	4	317- 320	8
Keppel Island	absent	1	334 - 336	16
North Arm	present	2	326 - 328	11
Pebble Island	present	5	313 - 340	25
Península Valdés	present	8	283 - 316	15
Sea Lion Island	absent	6	287 - 350	24
Stanley Common	present	7	313 - 316	15

**Table 1:** Summary of study sites detailing mammalian predator status, human activity score (1 = lowest, 8 = highest), and sampling date ranges and sample sizes for each site (total  $n = 130$  nests)

### *Spacing of nests*

Because information on predator approaches can be obtained by prey animals directly, or indirectly via observing the responses of other individuals (e.g. alarm calls; Griffin, 2004), it is important to consider indirect sources of such information. In the Two-banded Plover the non-incubating (male) bird is seldom present in the nesting territory during the day and is thus unlikely to influence the anti-predator behaviour of his mate by responding to potential predator approaches. However, because the actions of conspecifics at nearby nests might affect expressed flushing distances, we controlled for variation between nests in the distance of each nest from its nearest known neighbour (Nearest Neighbour Distance, henceforth NND); this allowed us to assess the possibility that individuals at closely-spaced nests might have had access to additional information from neighbouring birds during trials. NND was estimated for each nest using GPS data, and was included as a covariate in the analysis of flushing distance.

### **Data analysis**

Because each site had a unique level of human activity, a mixed modelling approach with 'site' as a random factor was not possible. We thus took two approaches: first, we performed an analysis in which individual nests ( $n = 130$ ) were the unit of analysis. Secondly, we performed a conservative analysis in which site ( $n = 8$ ) was the unit of analysis, and a single (mean) flushing distance datum was used for each site.

Data were transformed (flushing distance was square root transformed, and NND and nest isolation were  $\log_{10}$  transformed) to meet parametric model assumptions (normality and homoscedasticity), and analysed using General Linear Models implemented in Program R (R Core Development Team, 2005).

For each analysis, we first fitted a full model that included all main effects and likely two-way interactions. From each full model we then sought the minimum adequate model (henceforth MAM) using a backward stepwise procedure to remove terms which did not contribute significantly to the explanatory power of the model according to Akaike's Information Criterion (AIC); at each step we tested the effect of deleting each term on model deviance, and term deletions were rejected if AIC increased.

With 'nest' as the unit of analysis, flushing distance (m) was the continuous response variable; the full model included nest isolation ( $\log_{10}$  m), nest age (d), NND ( $\log_{10}$  m), Julian calendar date, and human activity rank (1-8) as continuous variables, mammalian predator status, clutch size and observer identity as two-level factors, and first-order interactions between human activity, nest isolation and mammalian predator status. With 'site' as the unit of analysis, mean flushing distance was modelled as a function of human activity, mammalian predator status, and the interaction between the two. In all cases, each factor, covariate and interaction term used one degree of freedom. As the use of a different observer in Península Valdés presents a potential confound, we repeated the full and reduced models with the Península Valdés subset



excluded; the results were robust to the removal of these points, with similar effects and significance levels.

Finally, to ensure the robustness of both MAMs to possible errors in the ranked human activity variable, a series of alternative rankings were created in which single pairs of adjacent ranks were switched (e.g. in the first alternative ranking, sites originally allocated ranks 1 and 2 were re-assigned ranks 2 and 1 respectively, while ranks from 3 to 8 remained unchanged). In all of these MAMs, all terms remained highly significant with similar effect sizes when the alternative rankings of human activity were substituted for our original rankings.

## RESULTS

### Nest as unit of analysis

The full model for flushing distance explained 53% of the variation in flushing distance, with significant effects of clutch size and the interaction between human activity and mammalian predator status, and a large but statistically nonsignificant main effect of mammalian predator status (Table 2).

Effect	Estimate	Std Error	F	p
(intercept)	-1.923	4.756	-0.404	0.687
clutch size	0.762	0.307	2.483	0.014
nest isolation	1.920	1.373	1.398	0.165
mammalian predators	4.559	2.649	1.721	0.088
human activity	-0.047	0.772	0.061	0.951
nest age	-0.015	0.017	-0.895	0.373
observer ID	-0.293	1.102	-0.266	0.791
time of season	0.001	0.012	-0.005	0.999
nearest neighbour distance	-0.141	0.314	-0.449	0.654
mammalian predators x isolation	-1.183	0.914	-1.294	0.198
mammalian predators x human activity	-0.390	0.172	2.264	0.025
human activity x isolation	0.036	0.250	0.145	0.885

**Table 2:** Predictors of flushing distance ( $\sqrt{m}$ ) in nesting Two-banded Plovers: Full GLM with individual nests (n = 130) as unit of analysis

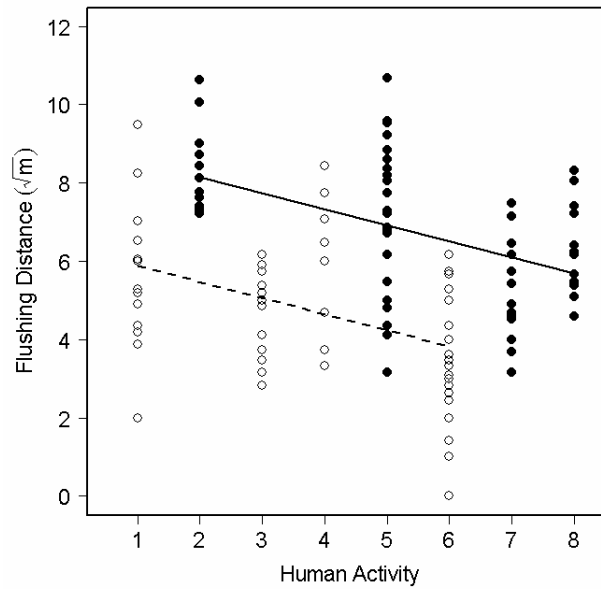
The MAM explained 50% of the variation in flushing distance using 7 fewer degrees of freedom, with a lower AIC and no significant increase in deviance compared to the full model (AIC 480.13 versus 485.59, ANOVA:  $F = 1.145$ ,  $p = 0.340$ ). In the MAM, mammalian predator status, human activity and nest isolation were all highly significant predictors of flushing distance, and clutch size had a small but significant effect (Table 3a). Flushing distances were greater when mammalian predators were present, human activity was low, nests were more isolated and clutches contained more than two eggs (Figs 2a - 4).

### Site as unit of analysis

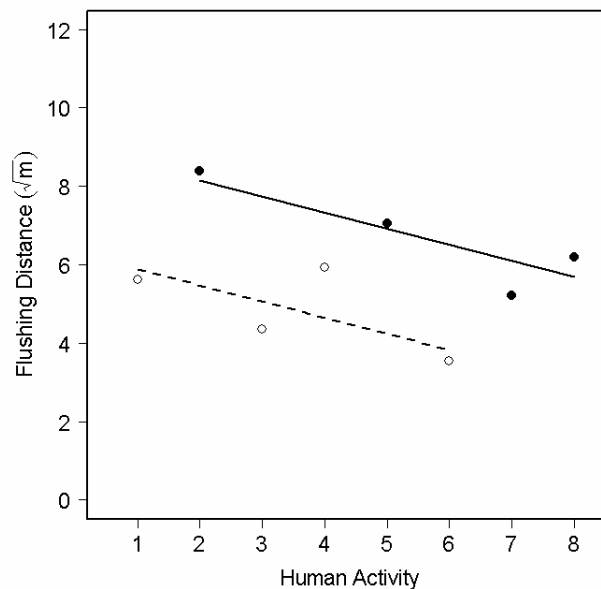
The results remained consistent with respect to mammalian predator status and human activity when we used site ( $n = 8$ ) as unit of the analysis. The full model included mammalian predator status, human activity and the interaction between the two variables. Removal of the interaction term resulted in a reduction of AIC (AIC 23.87 versus 25.59) and no significant increase in deviance (ANOVA:  $F = 0.141$ ,  $p = 0.727$ ), thus only the main effects were included in the MAM (Table 3b). Consistent with the preceding analyses, flushing distances were greater at sites where mammalian predators were present and human activity was low (Figure 2b).

	Effect	Estimate	Std Error	<i>F</i>	<i>p</i>
(a)	(intercept)	-0.899	0.974	0.923	0.358
	clutch size	0.722	0.302	2.392	0.018
	nest isolation	0.918	0.292	3.141	0.002
	mammalian predators	2.707	0.293	9.233	< 0.001
	human activity	0.411	0.066	6.241	< 0.001
(b)	(intercept)	6.298	0.645	9.769	< 0.001
	mammalian predators	2.677	0.649	4.128	0.009
	human activity	-0.411	0.142	2.906	0.034

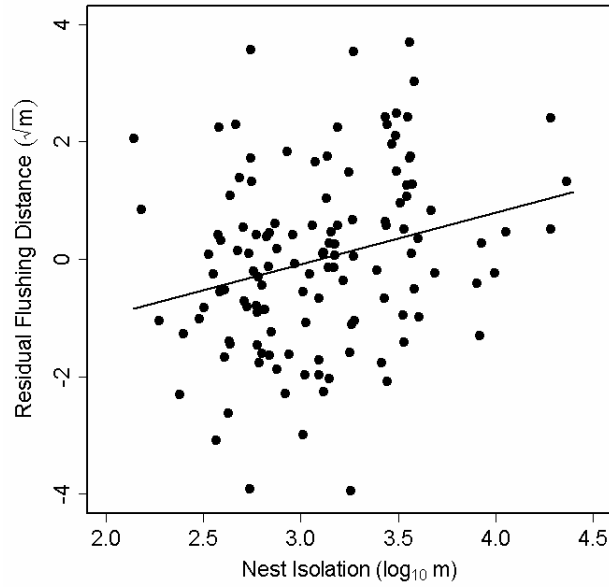
**Table 3:** Predictors of flushing distance ( $\sqrt{m}$ ) of nesting Two-banded Plovers: Minimum Adequate GLM's (a) with individual nests ( $n = 130$ ) as unit of analysis and (b) with site mean values ( $n = 8$ ) as unit of analysis



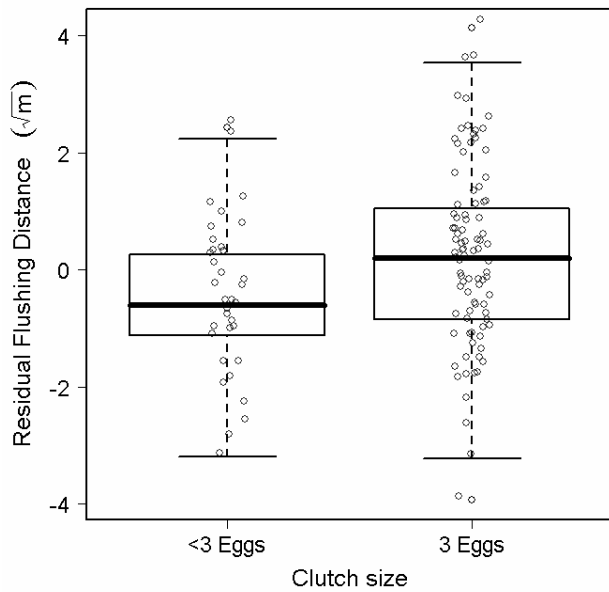
**Figure 2a:** Relationship between mammalian predator status, human activity score (1 = low, 8 = high) and flushing distance, with data and model fits with nest as unit of analysis. Solid symbols and line are from sites with mammalian predators; open symbols and dashed line from sites without.



**Figure 2b:** Relationship between mammalian predator status, human activity score (1 = low, 8 = high) and flushing distance, with data and model fits with site as unit of analysis. Solid symbols and line are from sites with mammalian predators; open symbols and dashed line from sites without.



**Figure 3:** Regression of nest isolation (distance to nearest settlement,  $\log_{10}$  m) versus flushing distance (residuals, after controlling for other variables in MAM)



**Figure 4:** Relationship between clutch size ( $n = 95$  nests with 3 eggs and 35 nests with fewer than 3 eggs) and flushing distance (residuals, after controlling for other variables in MAM)

## DISCUSSION

Our results suggest that incubating Two-banded Plovers are habituated to human activity, because flushing distances in response to humans are decreased in areas where human

activity is high. In addition, flushing distances increased with the presence of mammalian predators suggesting generalisation or sensitisation to potential predators. The latter result is of particular interest, because it implies that introduced mammalian predators can increase the effects of non-lethal human disturbance.

### **Non-lethal disturbance in breeding birds**

The fitness consequences of increased flushing distances in breeding birds are not known (Lima, 2009). Other things being equal, increased flushing distances should result in increased frequency of flight because the paths of disturbance stimuli will intersect a large-radius circle more frequently than a smaller-radius circle. Increased flushing distance may also be associated with longer intermissions because the individual may have to delay its return for longer before the stimulus is a tolerable distance from the nest. Long and frequent intermissions in incubation can be detrimental to developing embryos, as the resulting fluctuations in temperature can alter metabolism, increase incubation time, and reduce egg viability (Olson et al., 2006; Webb, 1987); the re-warming of eggs is also energetically expensive for adults (Nilsson et al., 2008; Reid et al., 2002). It is thus likely that increased flushing distances are costly to both the adults and their offspring. When flight occurs in response to non-lethal stimuli there are no concomitant benefits (in terms of reduced predation) which might mitigate the energetic and developmental costs incurred by the parent and offspring. In fact, parental activity may sometimes increase the risk of nest predation as the attention of visual nest predators may be attracted by movement (Muchai and du Plessis, 2005). Habituation provides a mechanism for reducing the frequency with which these costs are incurred, as repeated exposure to non-lethal stimuli can allow individuals to better distinguish them from genuine predators. Consistent with our prediction of habituation to human disturbance, we found flushing distances were lower at sites with high levels of human activity and when nests were located close to centres of human activity.

### **Effect of cats**

Our results also suggest that birds react to the presence of cats by increasing flushing distances in response to approaching humans, and we can think of no biologically relevant confounding variable that might sensibly explain this trend. For instance, there were no consistent differences in topology, nesting habitat or avian predator communities between sites with and without cats (Woods and Woods, 1997), and flushing distances were no different at nests that had nearby neighbours than at nests that were more widely spaced. The latter point indicates that birds were unlikely to have varied their anti-predator behaviour in response to information obtained from nearby nests during the course of the study.

The mechanism by which mammalian predator presence might affect disturbance tolerance is unknown. There is strong evidence that some prey species increase vigilance when

predators are abundant (Caro, 2005). It is thus possible that the observed increase in flushing distances at sites with introduced cats reflects increased vigilance, resulting in an earlier time-of-detection of approaching humans (the 'perceptual limit hypothesis' of Ydenberg and Dill, 1986). As we did not record vigilance behaviour, we are unable to assess this hypothesis although it seems unlikely that incubating plovers were very long unaware of something as conspicuous as a directly approaching human in open habitat. Another possible explanation might be local adaptation, which can occur very quickly in response to powerful selection pressures such as predation (Losos et al., 2004). However, the cursorial ability of Two-banded Plovers, the short distances between the Falkland Island study sites, and the relatively short time since the extirpation and introduction of native and non-native mammalian predators (~150 years) all suggest that the observed variation is unlikely to be evolved: it more likely results from ontogenetic naïveté (sensu Cox and Lima, 2006) in individuals which have not been exposed to mammalian predators. The observed variation thus implies a learning mechanism. A feasible mechanism has recently been highlighted, in which a prey animal experimentally subjected to an aversive experience with a model predator subsequently increases anti-predator behaviour towards a different model that resembles the first (the 'predator recognition continuum hypothesis'; Ferrari et al., 2007; Ferrari et al., 2008; Griffin et al., 2001). It is worth noting that an 'aversive experience' need not necessarily be a predation event or even witnessing a predation event, but that social learning of predator recognition, for example via alarm calls, can be extremely efficient (Griffin, 2004). The Two-banded Plover does give alarm calls, and is also thought to be long-lived (St Clair et al. submitted), giving individuals plenty of time to assimilate information from conspecific alarms, or by witnessing or experiencing predation attempts by predators including cats. A recent study on mammals even suggests that information on predation risk can be communicated before birth; variation in anti-predator behaviour may arise from adaptive maternal effects following elevated predation risk during the parental generation (Sheriff et al., 2009). Finally, there is evidence that a generalised increase in anti-predator behaviour in response to predator introduction can be mediated by the endocrine system: iguanas sharing islands with introduced cats show an increase in the glucocorticoid hormones associated with anti-predator behaviour, leading to increased flight initiation distances in response to approaches by (non-predatory) humans (Berger et al., 2007; Rödl et al., 2007).

### **Reproductive value**

We observed a positive association between flushing distance and clutch size, but no association between flushing distance and the age of the eggs. Relationships between flushing distance and clutch size and age are often interpreted as increased parental investment when the reproductive value of the clutch is relatively high (Lima, 2009; Montgomerie and Weatherhead, 1988). However, the sign of the relationship between flushing distance and clutch size in the Two-banded Plover differs from some other studies of anti-predator behaviour of nesting birds, in which flushing distances decrease with increasing reproductive value and

delayed flight is interpreted as a sign of increased parental investment (e.g. Albrecht and Klvaňa, 2004). The difference can be reconciled by considering the difference between cryptic species with conspicuous eggs which rely primarily on adult crypsis to avoid nest predation (such as ducks), and species with conspicuous adults and cryptic eggs which nest in open areas of low vegetation (such as the Two-banded Plover) that rely primarily on active avoidance. Clearly, in the former group, early flushing in response to a distant but approaching nest predator would only slightly alter risk to the parent but would *increase* the risk to the eggs; in the latter group, early flushing would also have a small effect on the risk faced by the parent, but would substantially *reduce* the risk to the eggs. The 'parental investment' term faced by parents of such species is thus not (as in ducks) the increased risk of predation they are prepared to incur by delaying flushing, but the energetic cost of fleeing the eggs earlier – and thus more frequently – and re-warming them when the danger is past (Baudains and Lloyd, 2007). Interestingly, this energetic cost is likely to increase with the size of the clutch (Reid et al., 2002; Thomson et al., 1998), which perhaps explains why we observed an increase in flushing distance with clutch size but not with clutch age.

## Conclusions

Our results suggest that spatial variation in the distribution of predators and humans, together with intrinsic factors such as clutch size, can influence the expression of anti-predator behaviour in response to human approaches; these results are additive and robust to the level of analysis and potential errors in human activity scores. Although studies in reptiles have demonstrated comparable effects of predator presence on disturbance tolerance (Berger et al., 2007; Rödl et al., 2007; Stone et al., 1994), we believe ours is the first to show this effect in an avian species. Although generalisation between potential predators can clearly be adaptive (Ferrari et al., 2007), it may also be an important cause of vulnerability to human disturbance (Frid and Dill, 2002). We suggest that future studies should explore the generality of our results among different taxa and ecosystems in nature. Further experimental work is also needed to investigate the underlying learning mechanisms. Given the potential for non-lethal disturbance to impact substantially on fitness (e.g. Amo et al., 2006; Beale and Monaghan, 2004; Kerbiriou et al., 2009) our work may have important implications in terms of conservation of prey populations. For example, a recent trend in restoration ecology is the re-establishment of locally extinct predator populations (Caro, 2007), but in the light of our study conservation managers may wish to consider the possibility that following predator re-introduction, sympatric prey species could suffer not only increased predation, but potentially also increased levels of disturbance from sources which were previously tolerated such as human walkers. Similarly, eradication or control of non-native predators may also result in reduced non-lethal disturbance of native prey animals, and this potential benefit should be considered when prioritising such interventions (Atkinson, 1989). Future field studies will also benefit from considering sites with different combinations of mammalian predators, and by recording the density of different

predator populations rather than using presence/absence data. Understanding the complex interactions between prey animals, their predators, and non-lethal sources of disturbance is increasingly important, as introduced predators and anthropogenic disturbance become ever more ubiquitous (Atkinson, 1989; Baudains and Lloyd, 2007). We suggest that these investigations of anti-predator behaviour will require a variety of comparative and experimental approaches, and that ground-nesting birds in open habitats (such as plovers) provide an excellent study system.

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**Chapter 6:      RESPONSES OF AN ISLAND ENDEMIC INVERTEBRATE TO RODENT  
INVASION AND ERADICATION**

James J.H. St Clair, Sally Poncet, Dan  e K. Sheehan, Tam  s Sz  kely & Geoff M. Hilton

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DS:     Fieldwork, Comments (5%)

GH:     Comments (5%)

TS:     Comments (5%)

## ABSTRACT

Invertebrates dominate many terrestrial ecosystems in terms of biomass, and also structure ecosystems through their roles as pollinators, detritivores, primary consumers, predators and prey. Invasive rodents (rats and mice) are known to have detrimental effects on many island invertebrates, although these effects are seldom quantified or ecologically understood. Here we provide evidence of the effects of invasive rats on island invertebrate populations using a large-scale natural experiment. We investigated the effects of invasive rats *Rattus* spp. on Falkland camel crickets *Parudenus* spp. in the Falkland Islands (South Atlantic) by comparing an index of camel cricket relative abundance between 18 rat-infested islands, 6 rat-eradicated islands and 13 naturally rat-free islands (in total, 37 islands). Our study provided two key results. First, camel crickets were estimated to be up to an order of magnitude more abundant on rat-free islands than on rat-infested or rat-eradicated islands. This effect varied according to vegetation type: the difference between rat-infested and rat-free islands was larger in native tussock grass *Poa flabellata* than in other vegetation types. Second, camel cricket populations recovered after rat eradication, since the relative abundance of camel crickets on rat-eradicated islands was intermediate between those of naturally rat-free and rat-infested islands, and among the rat-eradicated islands relative abundance was lowest where rats had been cleared most recently. Our results demonstrate severe suppression of an island endemic invertebrate by invasive rodents, and its prompt recovery after rodent eradication. The impacts of invasive rats on *Parudenus* camel crickets, a locally superabundant and large-bodied taxon (body length > 20 mm), may lead to fundamental changes in nutrient cycling and to a cascade of ecological changes, given their likely role as a food source for terrestrial predators including the globally vulnerable endemic Cobb's wren *Troglodytes cobbi*.

## INTRODUCTION

A number of studies indicate that predation by introduced rodents can severely affect island invertebrate populations, resulting in local suppression or extinction (Gibbs, 2009; Towns, 2009). The majority of these studies come from New Zealand, although a handful from other regions suggest that rodent impacts on island invertebrates may be geographically widespread (e.g. Hadfield and Saufler, 2009; Palmer and Pons, 1996). Furthermore, such impacts may be ecologically important - not only do island invertebrate species often exhibit a high degree of endemism and thus have inherent conservation value, but they can also be vital for ecosystem functioning, with key roles as pollinators, detritivores, primary consumers, predators and prey (Kim, 1993; Seastedt and Crossley, 1984). Despite this importance, island invertebrates are frequently overlooked in invasive species research and management, with a disproportionate bias in attention and effort towards the conservation of charismatic vertebrate species (Clark and May, 2002). Although the rate and scope of rodent eradications from islands across the globe is accelerating (Howald et al., 2007), quantitative information on the impact of rodents and rodent eradications on island invertebrates remains scarce (Towns et al., 2006), despite their potential utility in justifying, prioritising and assessing the conservation benefits of such operations.

Little is known about the effects of invasive rodents on the native biota of the Falkland Islands, a South Atlantic archipelago of several hundred islands which contains no extant native mammals. One study has demonstrated that most native songbird species are either suppressed or extirpated on islands where rats are present, and similar effects on burrowing seabird populations may occur (Croxall et al., 1984; Hall et al., 2002). Such impacts have precipitated a program of rat eradications, and subsequent monitoring of a handful of the rat-eradicated islands has shown a partial recovery of passerine populations (Woods et al, in prep). However, the effect of invasive rats and their eradication on the islands' invertebrate fauna has never been studied.

We studied the effects of rat invasion and eradication on the Falkland Islands' endemic *Parudenus* camel crickets, which are among the largest terrestrial invertebrates to occur there, attaining a body length of over 20 mm (Jones, 2004). As well as being large-bodied, camel crickets are both widespread and remarkably abundant in the islands and are thus likely to be fundamentally important to the native ecosystem (Gaston and Fuller, 2008). Likely functions include nutrient cycling and acting as a key prey group for vertebrate predators, roles which the Orthoptera are known to fulfil in other systems (Belovsky and Slade, 2000; Kopij, 2005; Samways, 1997). Consistent with importance as prey for native predators, camel crickets are thought to be a significant prey resource for several Falklands endemic songbird taxa (Cawkell and Hamilton, 1961; Jones, 2004).

We anticipated rat impacts on Falkland Islands camel crickets for several reasons. Firstly, a negative association between the presence of invasive rats and the abundance of camel crickets has been anecdotally noted (Alex Jones, pers. comm). Secondly there is evidence from

studies elsewhere that population-level impacts of rats may be most severe for large-bodied invertebrates, particularly those with a rodent-free evolutionary history (Gibbs, 2009). Thirdly, the New Zealand case study suggests that Orthopterans – especially the suborder Ensifera, which includes both giant weta and camel crickets – are particularly vulnerable to predation by introduced rats (Towns, 2009). Finally, rats are known to prey on camel crickets in the Falkland Islands, as evidenced by remains in rat stomach contents (Peter Carey, pers. comm.) and droppings (James St Clair, pers. obs).

To investigate the apparent association between rats and camel crickets we used a cross-island quasi-experimental approach, by installing standardised grids of pitfall traps on islands which were rat-infested, naturally rat-free, or recently cleared of rats. By incorporating islands on which rats once occurred but have since been eradicated into the natural experimental design, factors such as anthropogenic disturbance which might simultaneously favour (for example) rat presence and camel cricket absence can be more confidently discounted. The design also allowed us to investigate whether, if camel crickets are affected by rat presence, the effect can be reversed by rat eradication. The reversal of the detrimental effects of invasive species is a key objective of eradication programs, and of restoration ecology in general, but this reversibility is often assumed rather than explicitly tested (Simberloff, 1990).

## **METHODS**

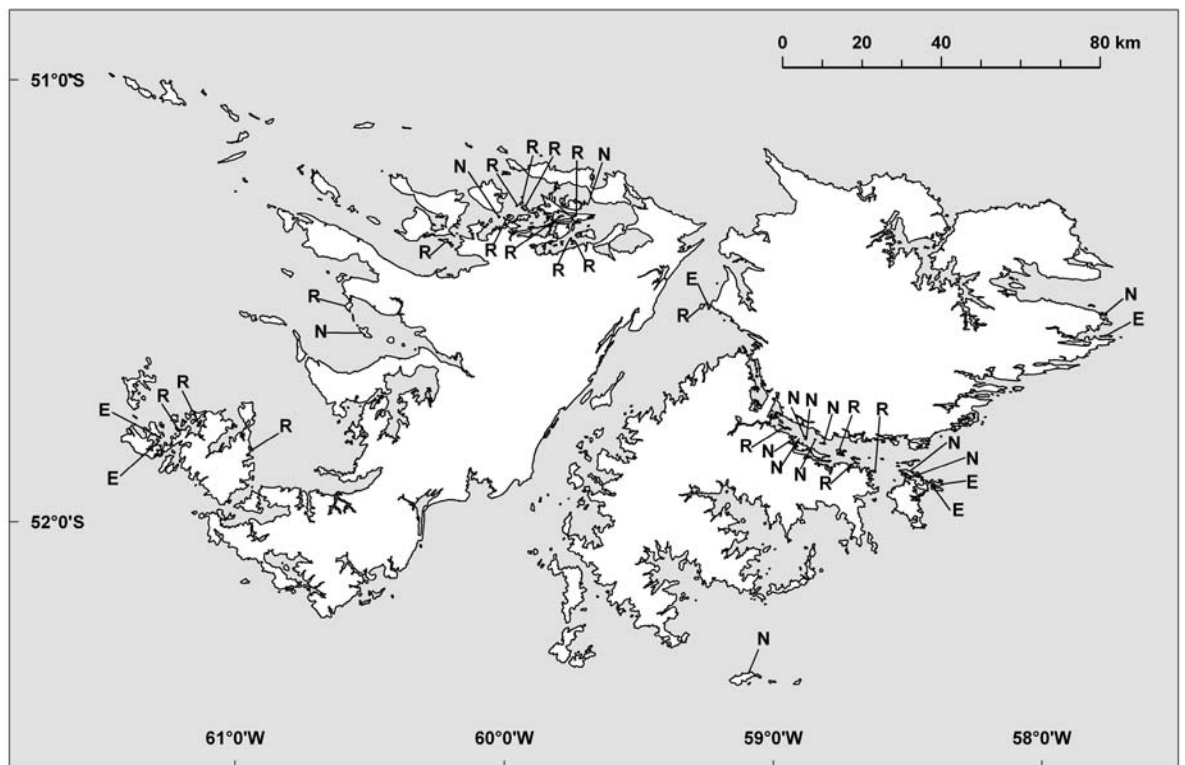
### **Study sites**

The Falkland Islands are an archipelago of two principal islands (East and West Falkland) and over 750 smaller islands in the South Atlantic Ocean, located approximately 500 km East of continental South America. The anthropogenic introduction of exotic rodents (*Rattus norvegicus*, *R. rattus* and *Mus musculus*) to many of the Falkland Islands has created a natural experiment; furthermore, since 2001 *R. norvegicus* populations have been successfully eradicated from twenty islands (Poncet et al, in prep). During the Austral summer of 2008/09, we visited 37 islands across the Falkland Islands archipelago (Fig. 1). Of these, 13 were naturally rat-free, 18 contained extant rat populations, and six had been the subject of successful rat eradication programmes. Sampled islands ranged from 1 to 905 hectares, with a median size of 16 ha. Data on rat presence was confirmed in all cases by searching for sign including burrows, droppings and tracks. In the Falkland Islands, these signs are usually very obvious and it is possible to categorise an island as rat-free or rat-infested within a few minutes of arrival.

## Study species

The Falkland camel crickets *Parudenus* spp. are a genus endemic to the Falkland Islands, and are the only Orthoptera to occur there (Jones, 2004). The taxonomy of the *Parudenus* genus has not yet been resolved (Eades and Otte, 2010), and as the genus may prove monotypic (containing only one species, *Parudenus falklandicus*) we henceforth use the term 'camel crickets' for the taxon.

No attempt was made to identify the species of rat at each island, but as *R. rattus* is only known to occur on New Island (Woods and Woods, 1997), which was not sampled, it is probable that our study islands harboured only *R. norvegicus*. The distribution of *M. musculus* is relatively unknown and difficult to determine, and while we avoided sampling rat-free islands known to contain mice, mouse presence on some of our study islands is likely.



**Figure 1:** the Falkland Islands, showing distribution of study islands. 'R' denotes rat-infested; 'N' denotes naturally rat-free; 'E' denotes rat-eradicated.

## Data collection

At each island, we installed a grid of pitfall traps consisting of eight lines of five traps, each line perpendicular to the coast. In each line, the five traps were placed at 0, 5, 20, 50 and 100 metres relative to the first permanent vegetation above the high tide line. On very small or narrow islands (< 200m wide) the final trap was omitted, giving a line of four traps at 0, 5, 20



and 50 metres inland. The spacing of traps within traplines was coastally biased because in the Falkland Islands the distributions of both rats and Tussac grass (a key native habitat) are also coastally biased (Peter Carey & Darren Christie, pers. comms). Trap lines were placed 200 metres apart, and on smaller islands (< 1600 m circumference) this spacing was reduced as necessary to accommodate all eight lines of traps. In statistical models we used island area to control for the reduction of the study area on the smallest islands, and for potential effects of island area on camel cricket density.

Each pitfall trap consisted of a plastic cup, 8.5 cm depth and 6.5 cm diameter at the lip (volume 215 ml), countersunk to soil level and containing water to a depth of ~ 3 cm. The water contained a drop of washing-up detergent to reduce surface tension. Each trap had a mesh cover, fixed with wire 2 cm above the trap to deter interference from larger animals. At each trap, we recorded the distance from the shore (in m), and the dominant vegetation type within a 1 m radius of the trap. Five vegetation classes were included; Tussac grass *Poa flabellata* (41 % of traps); Diddle-dee *Empetrum rubrum* (21 %); Bare soil (8 %); and finally, all remaining plant cover types – generally a mixture of grasses, sedges and herbaceous perennials – were divided into two sward categories, Short (< 15 cm; 26 %) and Long (> 15 cm; 4 %). As vegetation might also affect camel cricket populations at larger spatial scales than our ‘vegetation type’ factor could detect, two further explanatory variables were created and scored for each island; a two-level ‘grazing status’ factor (island currently grazed or ungrazed), and a continuous explanatory variable comprising the proportion of pitfall traps (arcsine-transformed) on each island that were located in Tussac grass, which is regarded as the natural climax vegetation for coastal regions in the Falkland Islands (Woods and Woods, 1997). We left each trap for two nights, although in some cases we were unable to collect traps until three (n = 3 islands) or four (n = 2 islands) nights had passed. We used this extremely short trapping duration to reduce possible effects by which early captures affect the probability of later captures, including the ‘digging-in’ effect by which, over time, pitfall traps deplete invertebrate populations in their immediate vicinity (Digweed et al., 1995; Southwood and Henderson, 2000). After collection, all traps were scored as present or absent with respect to camel crickets.

Because of a spatial bias in the distribution of sampled islands – with 72% of sampled rat-infested islands located around West Falkland, and 70% of sampled rat-free islands located around East Falkland (Fig. 1) it was necessary to control for any potential pre-existing geographical bias in camel cricket distribution. To this end a two-level ‘island location’ factor was created, to which islands were assigned according to their location off East or West Falkland.

### **Data analysis**

Presence/absence of camel crickets in pitfall traps formed the response variable. Binary data were used for two reasons; firstly, such data are free from any bias introduced by potential

conspecific attraction - in which individuals may be more likely to enter a trap which has already captured one or more crickets (Southwood and Henderson, 2000) - and secondly the approach is highly conservative, giving equal weight to traps containing one or many camel crickets and requiring fewer assumptions about data structure (Crawley, 2007). Data were analysed using generalised linear mixed models with binomial errors, fit using Maximum Likelihood in the lme4 package of Program R version 2.6.2 (R core development team, 2008).

Model simplification followed the suggestion of Crawley (2007) for non-orthogonal study designs: each individual term was deleted from the full model, and a  $X^2$  deletion test was used to compare the full model with the reduced version: term deletions were rejected if they caused significant increases in model deviance. The same simplification process was used for the pooling of factor levels. Terms which were retained in the minimum adequate model (henceforth MAM) are presented with the results of the  $X^2$  deletion test and the change in Aikake's Information Criterion (henceforth  $\Delta AIC$ , a measure of model log-likelihood penalised by additional degrees of freedom) that resulted from the deletion of the term from the full model.

#### *Model 1 - camel cricket capture success*

Camel cricket presence/absence at the level of the pitfall trap was modelled as a function of the continuous variables 'n trap-nights', 'island area' (log10 transformed), 'proportion of traps in Tussac grass' (arcsine transformed) and 'trap distance from shore' (square-root transformed), and of the categorical variables 'rat status', 'observer ID', 'vegetation type', 'grazing status' and 'island location'. First-order interactions between 'trap distance from shore', 'rat status' and 'vegetation type' were also included (as these were judged biologically feasible *a priori*), with 'island ID' retained as a random factor in all models. Initially, 'trap line ID' was included as a random factor nested within 'island ID', but the nested term had a variance of zero and was excluded from subsequent analysis following Bates (2010).

#### *Model 2 - camel cricket capture success, 'rat-eradicated' subset*

A second set of models were specified to investigate the effect of time since rat eradication on camel cricket capture success, using only the subset of islands from which rats have been eradicated ( $n = 217$  traps on 6 islands), and incorporating a new explanatory variable 'n years since [rat] eradication'. To avoid over-parameterising the initial model, terms that had been identified as unimportant using the full dataset in the first (model 1) simplification were excluded *a priori*. The terms 'n trap-nights' and 'rat status' were also omitted, as within the rat-eradicated data subset they contained no variation. Finally, 'n years since eradication' and its first-order interaction with 'vegetation type' were included. In the full model, camel cricket presence/absence at the level of the pitfall trap was thus considered as a function of 'n years since rat eradication', 'vegetation class', 'trap distance from shore', and first-order interaction

between 'vegetation class' and 'n years since eradication', with 'island ID' retained as a random factor.

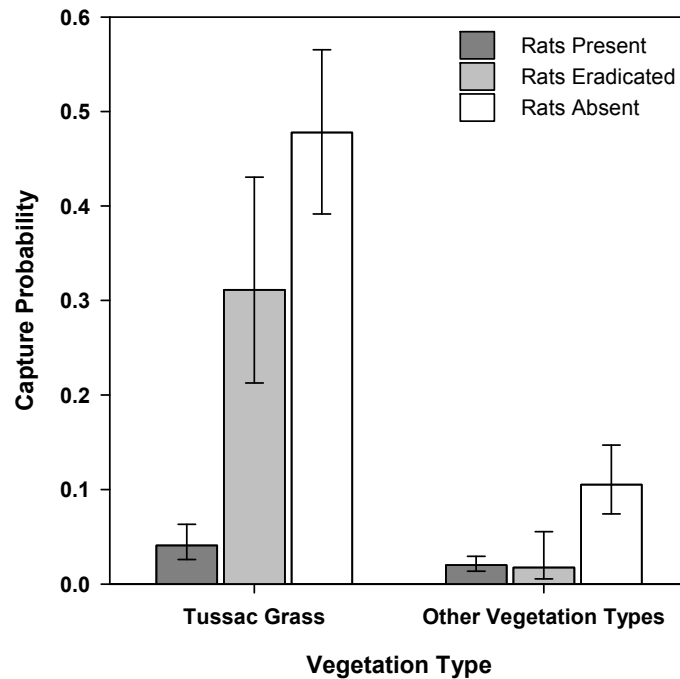
## RESULTS

809 camel crickets were captured during 2970 trap-nights on 37 different islands. Of 1365 traps retrieved, 269 captured at least one camel cricket. On seven islands, no camel crickets were captured in any trap; of these islands, five were classed as rat-present, two had rat-eradicated status, and none were classed as naturally rat-absent.

### **Model 1 Camel cricket capture success, all islands**

#### *Full model and simplification*

Removal of the terms 'observer ID'; 'n trap-nights'; 'proportion of traps in Tussac grass'; 'island area'; 'island location'; 'grazing status'; 'rat status x trap distance from shore' and 'vegetation type x trap distance from shore' from the full model did not significantly reduce explanatory power as determined by  $X^2$  model deletion tests and  $\Delta AIC$ , and so these terms were excluded from the minimum adequate model. Stepwise pooling of factor levels indicated that only one vegetation class ('Tussac grass') retained power as an explanatory variable; all other vegetation types were therefore pooled, forming a two-level vegetation-type factor ('Tussac grass' and 'other types'). Similarly, pooling of the rat-status levels 'naturally rat-absent' and 'rat-eradicated' did not reduce explanatory power, and these two factor levels were pooled to form a single 'rat-absent' factor level. The minimum adequate model thus contained a single continuous term ('trap distance from shore'), two two-level factors ('rat status' and 'vegetation type') and the interaction between 'rat status' and 'vegetation type'.



**Figure 2:** effect of rat status and vegetation type on the probability ( $\pm$  se) that pitfall traps contained one or more camel crickets; fits from a model identical to the MAM, but with 'rat-eradicated' and 'rat-absent' not pooled to form a single level as in the MAM. In calculating the model fits 'trap distance from shore' was set to zero. Pairwise comparisons within vegetation types were all highly significant ( $P < 0.0006$ ) apart from 'Rats Absent' vs 'Rats Eradicated' (both vegetation types) and 'Rats Eradicated' and 'Rats Present' (non-tussac traps only).

#### *Minimum Adequate Model*

The MAM indicated that camel crickets were less likely to be captured where rats were present than when they were absent, and more likely to be captured in Tussac grass than in other vegetation types (Table 1; Fig. 2). The significant interaction between vegetation type and rat status shows that the negative effect of rat presence was greater in Tussac grass than in other vegetation types. In both vegetation types, camel cricket capture success was lower when rats had been eradicated than when rats had always been absent (Fig. 2), although the difference was not statistically significant and the two factor levels were pooled in the MAM. Finally, there was a weak but highly significant effect of distance from the shore, with camel crickets more likely to occur away from the coast than adjacent to it after other variables were statistically held constant.

1a) full dataset				
Variable and Levels	Coefficient ± SE	ΔAIC	X <sup>2</sup> (df)	P
Intercept	- 2.416 ± 0.366	-	-	-
Trap distance from shore	+ 0.076 ± 0.027	3.39	9.392 (3)	0.0245
Rat status		10.88	16.889 (3)	0.0007
-Absent	-			
-Present	-1.494 ± 0.508			
Vegetation		49.78	55.785 (3)	< 0.0001
-Other types	-			
-Tussac grass	+ 2.104 ± 0.283			
Rat status x Vegetation		3.19	5.199 (1)	0.0226
-Absent, other types	-			
-Present, tussac grass	- 1.360 ± 0.568			

1b) rat-eradicated subset				
Variable and Levels	Coefficient ± SE	ΔAIC	X <sup>2</sup> (df)	P
Intercept	-11.018 ± 3.600	-	-	-
Years since rat eradication	+ 1.431 ± 0.611	6.56	10.566 (2)	0.0051
Vegetation		5.18	9.1918 (2)	0.0101
-Other types	-			
-Tussac grass	+ 2.652 ± 1.163			

**Tables 1a and 1b:** minimum adequate models of the effects of environmental variables on camel cricket pitfall-capture success (a) across islands with different rat status and (b) within the subset of rat-eradicated islands. Tables show coefficients (in logits) and associated standard errors. ΔAIC shows the increase that occurred when the variable and associated interactions were removed from the full model; X<sup>2</sup> statistic; degrees of freedom and P-values are for comparisons between full and reduced (variable-removed) models.

## **Model 2 Camel Cricket capture success, ‘rat-eradicated’ subset**

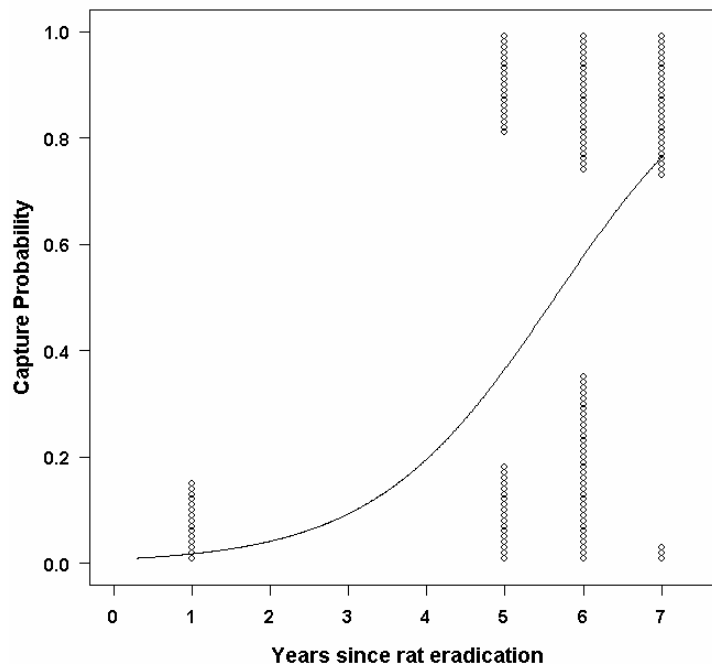
### *Full model and simplification*

Removal of the term ‘trap distance from shore’ and the interaction ‘vegetation type x *n* years since eradication’ did not significantly reduce explanatory power and so they were excluded from the minimum adequate model.

### *Minimum Adequate Model*

The number of years since rat eradication was a strong predictor of camel cricket capture success (Table 1b; Fig 3). This indicates that, when other variables such as vegetation type are controlled for, capture success increases during the years following rat eradication. It should be noted that sites were not evenly distributed along the x-axis (more islands were cleared 5-7 years ago than in the last 4 years) and the single site at which rats were eradicated one year

prior to sampling was clearly influential; however, when this site was excluded from the analysis, time since rat eradication remained a significant predictor of capture success ( $P = 0.0343$ ).



**Figure 3:** binomial logistic regression of cricket capture success against number of years since rodent eradication occurred, for traps in Tussac grass only; plot shows fitted line, with distribution of actual presence/absence data indicated by stacked points on the x-axes.

## DISCUSSION

We found that pitfall capture success of *Parudenus* camel crickets in the Falkland Islands was lower on rat-infested islands than on naturally rat-free islands, with the probability of capturing at least one camel cricket in a given trap estimated at over ten times higher for traps on rat-free islands in Tussac grass, and over four times higher in other vegetation types. Furthermore, the capture success on islands from which rats had been eradicated was intermediate between those of rat-infested and naturally rat-free islands, strongly suggesting a causal link between rat presence and camel cricket capture success. Consistent with this finding, capture success on rat-eradicated islands increased with the amount of time since the eradication took place.

The higher capture success in Tussac grass habitat, regardless of rat status, suggests that this is the favoured habitat of camel crickets as reported by other workers (Jones, 2004; Woods, 1970), and the interaction between rat presence and vegetation type in their effects on capture success is consistent with the finding that rat densities are also highest in Tussac grass habitat (Darren Christie, pers. comm.). The weak positive relationship between capture success and the distance from the shoreline may indicate an aversion to the elevated salinity (due to sea-

spray) of near-shore habitats, or possibly an effect of predation, as rats and most insectivorous songbirds occur at their highest density adjacent to the shore (Peter Carey, pers. comm., Woods, 1970).

### **Interpretation of pitfall capture success data**

Here we interpret pitfall capture success of camel crickets – within vegetation types – as an index of relative abundance. Several assumptions are implicit in this interpretation, which arise from the fact that the probability of pitfall capture is a function of both the abundance and activity level of the focal species; thus the relationship between relative abundance and capture success may be confounded by factors that affect activity levels. Potential confounds include relationships between early captures and the probability of subsequent captures, differences in vegetation structure between islands of different rat status, and behavioural responses to increased predation risk.

We are confident that the extremely short trapping duration and use of presence/absence data ensure that associations between early and late captures can be discounted as major sources of variation. We are also confident that the use of three vegetation-based explanatory variables ('vegetation type', 'proportion of traps in Tussac grass' and 'grazing status') has adequately controlled for any potentially confounding differences in the vegetation of rat-infested, rat-eradicated and naturally rat-free islands; in fact, once vegetation type was accounted for at the level of the pitfall trap, neither the proportion of Tussac grass in the study area or the grazing status of the island had explanatory power.

Finally, changes in prey activity levels may arise in response to differences in predator communities, as has been recorded in other Orthopteran taxa (Pitt, 1999; Rufaut and Gibbs, 2003). Although we cannot discount the possibility that rat presence causes reduced activity in *Parudenus* camel crickets, it seems improbable that such an effect would account for the order-of-magnitude differences in capture success between rat-infested and rat-free sites.

### **The impact of rats on camel crickets**

The difference in pitfall capture success between rat-infested and rat-free islands strongly indicates a severe reduction in camel cricket abundance when rats are present, and is likely to reflect top-down regulation of camel cricket populations by invasive rats via predation. This population suppression may serve to increase the risk of local extinction, particularly on small islands where absolute population size may be relatively small and the impacts of stochastic disturbance (e.g. weather, inundation, fire) correspondingly large. The capture of at least one camel cricket (with a moderate effort of ~ 80 trap-nights per island) on 13 of the 18 rat-infested islands we surveyed suggests that camel cricket populations are usually not driven to extinction by rat introduction, although occasional local extinctions are possible.

The high capture success on rat-free islands, particularly in Tussac grass (where approximately half of traps contained at least one camel cricket after only two days), suggests that camel crickets are remarkably abundant in these habitats. Invertebrate communities in the Falkland Islands are highly depauperate, and there is likely to be little redundancy within functional groups (Rosenfeld, 2002) – in fact, fewer than 300 insect species are known from the whole archipelago (Jones, 2004). On the basis of their abundance, large body size and phylogenetic and morphological uniqueness, it is probable that camel crickets have functional importance in terrestrial Falkland Islands ecosystems, and that their suppression by invasive rats is likely to indirectly affect other ecosystem properties. Studies elsewhere suggest that rodent impacts on detritivorous invertebrates may have far-reaching consequences for litter decomposition, nutrient cycling and other aspects of soil ecology (Fukami et al., 2006; Lawrence and Samways, 2003), while competition by invasive rodents for invertebrate prey may accelerate the decline or extinction of native predator species (Harris, 2009). The functional roles of camel crickets remain to be investigated, but may include the decomposition of dead vegetation and other detritus, predation on smaller invertebrates, and forming a prey-base for native insectivorous birds such as Cobb's Wren *Troglodytes cobbi* (Cawkell and Hamilton, 1961; Jones, 2004). We note that the majority of Falkland Islands songbirds are negatively associated with rat presence, in particular Cobb's Wren which never co-occurs with rats (Hall et al., 2002). Disjunct distributions of island birds and invasive rodents are usually attributed to predation of individuals or their nests, but evidence for a direct interaction is lacking in most cases – our results highlight another mechanism that should be given greater consideration, that of competition between native birds and invasive rodents for invertebrate prey.

### **Recovery after rat eradication**

Crucially, our results suggest that rat eradication has quick and measurable benefits for camel cricket populations, with capture success on islands from which rats have been eradicated resembling that on naturally rat-free islands more than that on rat-infested islands.

Given their likely roles as detritivores, predators and prey, the recovery of camel cricket populations after rat eradication should facilitate the recovery of other taxa and of whole-island ecosystems. Our data strongly suggest a prompt recovery of camel cricket populations following rat eradication, taking a few years at most. It should be noted, however, that on two islands from which rats had been eradicated no camel crickets were captured during our study. Although it is probable that the taxon does exist at relatively low abundances on these islands, its apparent absence raises a perennial caveat of restoration ecology; once a species has been extirpated from an island, it must first recolonise before recovery can begin (Townsend, 2009). The recolonisation ability of camel crickets is unknown, but they are entirely flightless, and natural recolonisation over long distances may well be an infrequent event. However, if it is ever confirmed that rats have extinguished a camel cricket population, translocation of new founders from nearby populations (following rat eradication) would be a straightforward solution.



## Conclusions and future directions

Very little is known about Falkland Islands terrestrial ecosystems in general, or *Parudenus* camel crickets in particular, and our results highlight some potentially productive research avenues. The number and distribution of *Parudenus* species, and whether each is affected equally by rat presence, remains unknown but should any distinct taxon prove to have a restricted or single-island range it would clearly be a priority for conservation management. The effects of mice and the potentially differing effects of the two *Rattus* species on camel crickets could not be distinguished with the data available, but such knowledge may prove useful in the prioritisation of rodent eradications. We did not attempt to determine the mechanism by which rats affect camel crickets, and although direct predation is the strongest candidate, quantitative dietary studies of rats – for preference in both early and late stages of rat invasion – are required to confirm the predation hypothesis.

We suggest that investigation of the functional roles of *Parudenus* camel crickets in the Falkland Islands would be rewarded by a deeper understanding of the indirect consequences of rat invasion, both for individual species and for ecosystem properties. The role of camel crickets in soil processes could be easily investigated experimentally, while their importance as a food for native birds would be straightforward to establish with quantitative diet studies.

Finally, our results suggest that the relatively well-documented suppression of many of New Zealand's endemic invertebrates following rodent invasion is not necessarily exceptional, and that comparable impacts on island invertebrates in other regions (which may be less distinct, both geographically and evolutionarily) could be more common and widespread than is usually appreciated. We suggest that practitioners of island conservation and restoration around the world should routinely consider the potential for rodent-invertebrate interactions, to complement the ongoing focus on charismatic vertebrate species.

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## **Chapter 7: THE IMPACTS OF INVASIVE RODENTS ON ISLAND INVERTEBRATES**

James J. H. St Clair

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JSC: Data Collection, Writing (95%)

TS: Comments (5%)

## ABSTRACT

The widespread invasive rodents *Rattus norvegicus*, *R. rattus*, *R. exulans* and *Mus musculus* have been implicated in the decline and extinction of hundreds of island endemic vertebrates, but their effects on island invertebrates are less well-known. Here I present the first global review of the subject, which confirms that large-bodied invertebrates are most at risk from these rodents, and that although a disproportionate number of studies (69 %) are from New Zealand, rodent-invertebrate impacts are geographically widespread. Currently many reported impacts are unquantified, come from uncontrolled and unreplicated designs, or rely on time-series with inadequate baseline data. In addition to basic improvements in study design, this review highlights a need for studies which investigate mechanisms of impact, or impacts across trophic levels. Mechanisms of impact can be both direct (mediated by predation) and indirect (involving intermediary species). Some studies also suggest knock-on effects of rodent-invertebrate interactions on ecosystem properties, and given the diverse ecological functions of invertebrates (as detritivores, primary consumers, predators, prey and pollinators), I suggest that an understanding of the interactions between invasive rodents and invertebrates in island ecosystems would contribute to effective conservation management.

## INTRODUCTION

The arrival of humans on remote islands is usually associated with a wave of extinctions in the native biota (Blackburn and Gaston, 2005; James, 1995; Steadman, 1997). Rodents that accompany human colonisation are a major contributor to this effect, likely accounting for more recent bird extinctions than any other single factor, and implicated in the extirpation of numerous small mammals, reptiles, amphibians and plant species (Athens, 2007; Blackburn et al., 2004; Harris, 2009; Johnson and Stattersfield, 1990; Jones et al., 2008; Towns et al., 2006).

Four rodent species are particularly notorious, having achieved enormous distributions due to their ability to hitch-hike on ships and canoes. Three of these (*Rattus rattus*, *Rattus norvegicus* and *Mus musculus*) have attained near-global distributions and a fourth (*Rattus exulans*) is widely distributed in the Pacific (Atkinson, 1985). Henceforth, 'invasive rodents' refers to these four species. Population-level effects (henceforth 'impacts') of invasive rodents on vertebrate populations have received considerable attention, but evidence from New Zealand also implicates invasive rodents in the decline and extinction of invertebrate populations, with many of New Zealand's endemic invertebrates are now confined to rodent-free offshore islands (Gibbs, 2009; Meads, 1990; Ramsay, 1978).

Despite this emergent New Zealand case study, the potentially global impact of invasive rodents on invertebrates has received little attention: a recent review of rat impacts cites only nine examples of rat-invertebrate interactions, largely from New Zealand study sites (Towns et al., 2006). This emphasis is consistent with the poor appreciation of invertebrates in conservation research: they comprise over 79% of all described animal and plant species, and yet only 11% of articles in leading conservation journals concern invertebrate taxa (Clark and May, 2002).

There are at least two major reasons to take invertebrate conservation seriously. Not only do island invertebrates often exhibit high levels of endemism and thus form a substantial component of biodiversity, but they can occupy key roles in ecosystems as detritivores, primary consumers, predators, prey, competitors, mutualists, pollinators and disease vectors. Effects at any of these functional levels may have knock-on effects on other ecosystem components (Dixon, 2009; Duthie et al., 2006).

Here, I overview the impacts of invasive rodents on island invertebrate populations across the globe. Using these data, I ask whether such impacts are likely to be a common feature of rodent invasion, and what can be learned from the geographical distribution, methodologies and results of the studies. I also present a summary of current knowledge of the diet of invasive rodents on islands. I searched the literature for studies which investigated population-level effects on island populations of invertebrates, including both island endemics and species with wider distributions. Within these criteria, I included records from well-controlled and replicated experiments to unquantified observations from single sites. I used ISI Web of Science and Google Scholar with combinations of search terms including

"Introduc\*", "Invas\*", "Exotic", "Eradicat\*", "Extinct\*", "Island", "Diet\*", "Rodent\*", "Rat\*", "Mouse", "Mus", "Invertebrat\*", and various high-level taxonomic names including "Mollusc\*", "Crustacea\*", "Arthropod\*" plus grammatical variations of terms where applicable. Having identified studies dealing with impacts and/or diet of invasive rodents on islands, their reference lists were scoured in turn. Systematic data collection was terminated in March 2010.

## THE DIET OF INVASIVE RODENTS

A comprehensive review of the diet of invasive rodents is beyond the scope of this review. However, three patterns in the rodent-diet literature are apparent and relevant to their potential impacts.

Firstly, the invasive rodent species are remarkably catholic in their diets, consuming vegetable matter, vertebrate animals of several different classes, and invertebrates. Few studies report no invertebrate dietary component (Witmer et al., 2006) whereas most studies report a significant invertebrate component (Cole et al., 2000; Drever and Harestad, 1998), and in the majority of these, invertebrates are the most frequently recorded food category (Caut et al., 2008; Chown and Smith, 1993; Copson, 1986; Daniel, 1973; Gales, 1982; Key et al., 1998; Le Roux et al., 2002; Miller and Webb, 2001; Smith et al., 2002). The potential for impacts on invertebrate populations is clear.

Secondly, invasive rodent populations frequently exhibit extreme dietary plasticity, with the relative contributions of different food types varying seasonally (Bunn and Craig, 1989; Copson, 1986; Le Roux et al., 2002; Miller and Webb, 2001), spatially (Erickson and Halvorson, 1990; Jones et al., 2003; Key et al., 1998) or both (Chown and Smith, 1993; Smith et al., 2002). Facultative plasticity and broad diets may not only facilitate establishment and persistence of invasive rodents in novel habitats, but may also allow predators to drive individual prey species to extinction while avoiding density dependent feedback effects.

Thirdly, a handful of studies report marine littoral invertebrates forming part of invasive rodent diet, particularly in rats (reviewed by Carlton and Hodder, 2003; Erickson and Halvorson, 1990; Navarrete and Castilla, 1993; Parisi and Gandolfi, 1974; Woods and Woods, 1997). The ability to exploit littoral resources may explain the frequently noted coastal bias in rat distribution (Erickson and Halvorson, 1990; Harper, 2006) and have major implications for rat density on very small islands (such as those favoured by breeding seabirds) in which most of the land area is close to the shore. In the Falkland Islands, the distribution of *R. norvegicus* is heavily biased towards the coast (Peter Carey and Darren Christie, pers. comms.), and studies of passerine bird distribution demonstrate that these rats have their greatest impacts on mainly coastal species such as Cobb's Wren *Troglodytes cobbi* and the Tussacbird *Cinclodes antarcticus* (Hall et al., 2002).

**Table 1:** studies investigating population-level impacts of invasive rodents on island invertebrates. Species codes: MM = *Mus musculus*; RR = *Rattus rattus*; RE = *Rattus exulans*; RN = *Rattus norvegicus*; R. spp – two or more *Rattus* species; FC – feral cats; OC – European rabbit. Sample sizes: n1 = treatment group, n2 = control group.

Rodent	Invertebrates	Study design and data collection	Impact of rodents, and details	Location	sample size	Publication
R. spp. & MM	giant predacious land snail <i>Powelliphanta traversi</i>	Baiting (monitoring and comparison)	Possible suppression; significant treatment effect (increase in snail population) in one of two sites. High temporal variation at all sites. Rat predation estimated to account for at least 20% of snail mortality.	Lake Papaitonga, North Island, NZ	n1 = 2 n1 = 2	(Bennett et al., 2002)
RN	invertebrates >4mm in length including beetle <i>Dorcus helmsi</i> , excluding amphipods and molluscs	Natural experiment (comparison)	Suppression (densities of most invertebrate taxa much higher on rat-free Gilbert Is. compared to rat-infested Breaksea Is.). On Breaksea, possible local extinction of the beetle <i>Dorcus helmsi</i> , which was not captured at all although fragments were abundant in the leaf litter.	Breaksea Island and Gilbert Island no. 6, NZ	n1 = 1 n2 = 1	(Bremner et al., 1984)
RE	endemic land snails <i>Amborhytida tarngensis</i> & <i>Placostylus hongii</i>	Prehistoric invasion (stratigraphy)	Local extinction (taxa went extinct on the island at approximately the colonisation time of RE. Evidence for an interaction is circumstantial)	Lady Alice Island, NZ	n1 = 1	(Brook, 1999)
RR & MM	All invertebrate taxa (order or family)	Baiting (comparison)	Suppression (rat density was reduced at the baited site and mouse density increased slightly. The baited site had higher catches of several taxa determined to be particularly important in Rat diets (Beetles, Cave Weta and Moths, and also Snails which were less important) while some smaller-bodied taxa (Ants, Woodlice, Springtails, Flies, Millipedes and also Crickets) were more abundant at the unbaited site. There were no significant differences for the remaining groups. Taxon diversity was significantly higher at the baited site)	North Island, NZ	n1 = 1 n2 = 1	(Craddock, 1997)
MM (+ FC)	weevil larvae flightless moths <i>Pringleophaga</i> spp.	Natural experiment (comparison)	Suppression of both groups, described as 'several times more abundant' on mouse-free Prince Edward Is., possible local extinction of <i>P. kerguelensis</i> on Marion Island. Mice estimated to take 21% of the standing crop of moth larvae annually. (NB trophic effect of cat-seabird-nutrients relationship is discussed)	Marion Island and Prince Edward Island Southern Ocean	n1 = 1 n2 = 1	(Crafford and Scholtz, 1987; but see Van Aarde et al., 2004)
R. spp.	Soil invertebrates <10mm identified to order level: nematodes (herbivorous, microbivorous and predacious), land snails, enchytraeid worms, rotifers, springtails, amphipod crustaceans and lepidopteran	Natural experiment (comparison)	Indirect suppression of all invertebrate taxa studied, although trend not significant in predacious nematodes. Unclear whether suppression at this taxonomic level results from species loss, reduced density of individuals, or both. Rats strongly affected nutrient levels and soil structure via	Various offshore islands, North Island, NZ	n1 = 9 n2 = 9	(Fukami et al., 2006)



	larvae		effects on burrowing seabird abundance; soil invertebrate effects are interpreted as downstream consequences.			
RE	tusked weta <i>Motuweta isolata</i>	Natural experiment (comparison)	Local extinction (species found only on rodent-free Middle Island, not on adjacent islands in the Mercury group which contain <i>R. exulans</i> . However, there is no evidence that its distribution was once broader)	Middle Island, Mercury Islands, NZ	n1 = 1	(Gibbs, 2002)
R. spp.	1 endemic snail ( <i>Partulina redfieldi</i> )	Local irruption (monitoring)	Suppression (85% decline in three years following appearance of rats at site)	Moloka'i, Hawaii, USA	n1 = 1	(Hadfield and Saufler, 2009)
R. spp.	endemic land snail <i>Achatinella mustelina</i>	Baiting (monitoring)	Suppression via selective predation on larger (mature) size classes. Population decline stopped 'abruptly' after rat poisoning began at the site.	O'ahu, Hawaii, USA	n1 = 1	(Hadfield et al., 1993)
R. spp, MM & Possums, Stoats, also present	Ground Weta, Cave Weta and Prowling Spiders	Baiting (monitoring and comparison)	No consistent treatment effects: some strong differences between sites, treatments, species and within-species size-classes. Tracking data suggests treatment (baiting) failed to suppress rodent populations relative to control sites in several cases.	Waitakere Ranges, North Island, NZ	n1 = 3 n2 = 6	(King, 2007)
RN	various littoral invertebrates including grazing molluscs and barnacles	Natural Experiment (comparison)	Increase in abundance of most groups (release from predation by gulls and oystercatchers, both of which were an order of magnitude more abundant on rat-free coastlines)	Aleutian Islands, USA	n1 = 8 n2 = 15	(Kurle et al., 2008)
R. spp. & MM	Various large weevil species (including <i>Anagotis stephensis</i> , <i>Anagotis rugosus</i> )	Prehistoric invasion (stratigraphy)	Suppression/local extinction: current distribution determined from museum collections, past distribution by stratigraphical examination of owl middens (n = 12). Several large weevil species now confined exclusively ( <i>Anagotis stephensis</i> ) or 'almost exclusively' ( <i>Anagotis rugosus</i> ) to rat-free offshore islands, while pre-invasion strata indicate distributions were once much wider.	Canturbury, South Island, NZ	n1 = 12	(Kuschel and Worthy, 1996)
RR	Flightless beetles <i>Hadramphus stilborcarpae</i> & <i>Dorcus helmsi</i>	Invasion (monitoring)	Local extinction (both species 'abundant' before rat introduction and apparently absent afterwards. <i>H. stilborcarpae</i> was 'teeming' in 1955; two expeditions in 1968 & 1969, ~20 yrs after <i>R. rattus</i> invasion, failed to find it alive. The weevil's host plant <i>Stilbocarpa lyallii</i> was also strongly impacted.)	Big South Cape Island, NZ	n1 = 1	(Kuschel and Worthy, 1996; Ramsay, 1978)
R. spp & MM	Seychelles giant millipede <i>Seychelleptus seychellarum</i>	Natural experiment (comparison)	Suppression or local extinction (millipedes superabundant on rodent-free Cousine, but 'extirpated or... very scarce' on mouse- and rat-infested islands including Praslin Island and Silhouette Island).	Cousine Island Seychelles	n1 = 1 n2 = 2 +	(Lawrence and Samways, 2003)
MM	various inc. new carabid beetle <i>Loxomerus</i> sp.; four other beetle species were recorded	Natural experiment	Suppression of most species on Bollons relative to mouse-free Antipodes; possible local extinction of <i>Loxomerus</i> spp.	Bollons & Antipodes Islands,	n1 = 1	(Marris, 2000)

	more frequently on Bollons Island than nearby mouse-infested Antipodes Island;	(comparison)	which was last seen as fragmentary remains in 1969	NZ Southern Ocean	n2 = 1	
RE	Stag beetles ( <i>Hemidorcus spp.</i> ), Weta (Orthoptera: Anostostomatidae), and other unspecified invertebrates	Eradication (monitoring)	Suppression ('major increases in... numbers of invertebrates' and discovery of species not known before eradication)	Rarotoka and Putauhinu Islands, NZ	n1 = 2	(McClelland, 2002)
RR	2 invasive snails ( <i>Achatina fulica</i> & <i>Euglandina rosea</i> )	Variation in rat abundance between sites (comparison)	Suppression (estimated minimum 7-20% of snail mortality) based on quantity of predation sign, correlated with rat abundance at different sites	Wai'anae mountains, Oahu Hawaii, USA	n1 = 2	(Meyer and Shiels, 2009)
RN	1 beetle ( <i>Mimopeus elongatus</i> ) 1 centipede ( <i>Cormocephalus rubriceps</i> )	Natural experiment (comparison)	Suppression on rat-infested Otata and local extinction on rat-infested Motohoropapa of both arthropod species (inferred from their presence on nearby rat-free David Rocks and Maria Island)	Otata and Motohoropapa Islands, NZ	n1 = 2 n2 = 2	(Moors, 1985; Watt, 1983)
RN.	1 land snail ( <i>Placostylus hongii</i> )	Invasion (monitoring)	Suppressed ('declined' after rat introduction – status described as 'nearly lost')	Aorangi Island, NZ	n1 = 1	(Moors, 1985)
MM	Cook's Strait Giant Weta <i>Deinacrida rugosa</i> and exotic land snail <i>Helix aspersa</i> ; also various 'other invertebrates'	Eradication (monitoring)	Suppression; although definitely present, snail catches were zero in all years prior to eradication and consistently high afterwards, based on 4 yrs pre- and 4 yrs post-eradication. Numbers of <i>D. rugosa</i> increased from <1 to >10 per 1000 trap nights. 'Other invertebrates' are mentioned as increasing in abundance and diversity after eradication, although not quantified.	Mana Island NZ	n1 = 1	(Newman, 1994) expanded results for <i>D. rugosa</i> in (McIntyre, 2001)
RR	5 endemic tenebrionid beetle spp.	Natural experiment (comparison)	Suppression or local extinction of five endemic species; two non-endemic species more likely to occur on rat-infested than rat-free islands	Various Islands Mediterranean, Spain	n1 = 25 n2 = 26	(Palmer and Pons, 1996)
RR	land crab <i>Gecarcinus ruricola</i>	Attempted eradication (monitoring)	Unclear; after attempted eradication and decrease in rat abundance, crab catches decreased from 0.85 to 0.46 per 100 trap nights, and then to 1.36.	Hardy Islet, Caribbean, Martinique	n1 = 1	(Pascal et al., 2004)
MM	'medium-sized flightless invertebrates'	Natural experiment (comparison)	Suppression or local extinction (unspecified 'medium sized flightless invertebrates' are lacking on Antipodes Island, but present on Bounty Island, which lacks mice, ~200km to the North)	Antipodes Island, NZ	n1 = 1 n2 = 1	(Patrick, 1994)
RR & MM	endemic Lord Howe Island stick insect ( <i>Dryocelus australis</i> )	Invasion (monitoring)	Extirpation (insect disappeared from Lord Howe Is. following rat introduction in 1918. Population now relict (9-35 individuals) on a tiny rat-free offshore islet (Carlile et al., 2009)	Lord Howe Island, Australia	n1 = 1 n2 = 1	(Priddel et al., 2003)

<i>R. spp.</i>	Morphotaxa > 3mm length	Baiting (monitoring)	No discernible treatment effect; ant abundance increased	Moehau, North Island, NZ	n1 = 2 n2 = 2	(Rate, 2009)
<i>RR &amp; MM</i>	2 large land snails ( <i>Placostylus bivaricosus</i> and <i>Gudeocoocha sophiae</i> )	Invasion (monitoring)	Suppression (both species were 'common' before the wreck of the SS Makembo; subsequently they became 'rare, confined to a few small colonies')	Lord Howe Island, Australia	n1 = 1	(Recher and Clark, 1974)
<i>MM</i>	various arthropods, particularly the flightless moth <i>Pringleophaga marioni</i>	(Estimated from diet)	Suppression (estimated consumption of 0.7% of 'standing crop' of arthropods per day, and 1% of <i>P. marioni</i> population per day leading to population decline)	Marion Island Southern Ocean	-	(Rowe-rowe et al., 1989)
<i>RE</i>	arboreal Weta <i>Hemideina crassidens</i>	Eradication (monitoring)	No clear population effect (Overall index of Weta abundance showed an increase for three years following eradication and a decrease in the fourth, possibly due to weather or density effects following rapid population growth. No pre-eradication data presented.)	Nukuwaiata Island, NZ	n1 = 1	(Rufaut and Gibbs, 2003)
<i>RE (+ RR?)</i>	2 land snails: the endemic <i>Placostylus ambagiosus</i> and introduced <i>Helix asperser</i>	Baiting (monitoring & comparison)	Suppression via reduced recruitment due to selective predation on medium-sized individuals. Population changes correlated with rat predation both through time at the study site, and spatially between the study and unbaited control site	North Island, NZ	n1 = 1 n2 = 1	(Sherley et al., 1998). Prehistoric rat predation of <i>P. ambagiosus</i> is also discussed by (Brook, 2000)
<i>RN &amp; RE</i>	all morphospecies >5mm in length	Eradication (monitoring)	Overall decrease in invertebrate diversity through time following eradication; site monitored for 2 yrs before and 3 yrs after eradication. Results highly variable and not consistent between taxa	Kapiti Island, NZ	n1 = 1	(Sinclair et al., 2005)
<i>RR</i>	2 littoral molluscs ( <i>Nerita picea</i> & <i>Littoraria pinctada</i> ), 1 crustacean ( <i>Grapsus tenuicrustatus</i> )	Eradication (monitoring)	Suppression (increase post-eradication, leading to "an abundance... where they were previously scarce")	Mokoli'i, Oahu, Hawaii, USA	n1 = 1	(Smith et al., 2006)
<i>R. spp.</i>	all families of arthropods	Baiting (monitoring and comparison)	No consistent trends; results variable.	Nelson, South Island, NZ	n1 = 3 n2 = 1	(Spurr, 1996)
<i>RE</i> <i>OC</i>	3 Cockroaches ( <i>Cerattoblatta</i> sp., <i>Parellipsidion lattipennis</i> , <i>Platyzosteria novaseelandiae</i> ); 3 beetles ( <i>Mimopeaus elongatus</i> , <i>Holocaspis mucronata</i> , <i>Ctenognathus novaezelandiae</i> )*; 1 earwig ( <i>Anisolabis littorea</i> )*; 1+ weta (Rhaphidophoridae);	Eradication and Natural experiment (monitoring & comparison)	Suppression or local extinction (on Korapuki island one pre- and one post-eradication survey completed; with the exception of the Orthoptera, of taxa listed, all were found in the second survey, but only <i>H. mucronata</i> was present in the first. This species increased in abundance. Natural experiment data: the orthoptera and other taxa marked with an asterisk were all found on rat-free Middle island, but not on Korapuki prior to eradication, while no species found on Korapuki were absent from Middle island.	Korapuki and Middle Islands, Mercury Islands NZ	n1 = 1 n2 = 1	(Townes et al., 1997)

	1 woodlouse*; 1 centipede ( <i>Cormocephalus rubriceps</i> )*; 1+ weta (Rhaphidophoridae)*; 2 Jerusalem crickets ( <i>Hemiadrius</i> sp., undescribed sp.)*;					(Towns et al., 1997 (continued))
<i>R. spp</i>	18 soil macro-invertebrate orders and 3 micro-invertebrate taxa (Rotifera, Enchytraeidae & Nematoda)	Natural experiment (comparison)	Indirect suppression of most invertebrate taxa studied; 16/18 macroinvertebrate orders were less abundant (per m <sup>2</sup> ) on rat-invaded islands (8 of these statistically significant), and 3/3 micro-invertebrate taxa also significantly less abundant. Taxon diversity of soil invertebrates was reduced. Differences associated in part with changes in soil chemistry and structure, due to reduction of burrowing seabirds by rat predation.	Various offshore islands, North Island, NZ	n1 = 9 n2 = 9	(Towns et al., 2009)
<i>RE (+ OC)</i>	1 scale insect ( <i>Coelostoma zealandica</i> )	Eradication (comparison & monitoring)	Suppression via prevention of host plant recruitment pre- eradication on rat-infested Korapuki Is, compared to rat-free Green & Middle Islands. Abundance of host plant and scale insects increased following rat (& rabbit) eradication.	Korapuki, Green and Middle Islands Mercury Islands NZ	n1 = 1 n2 = 2	(Towns, 2002)
<i>MM</i>	various soil invertebrates including <i>Pringleophaga</i> moths, weevils, lumbricids worms, spiders and terrestrial molluscs	Exclosure (comparison & monitoring)	Suppression of <i>Pringleophaga</i> larve (43% lower biomass in exclosures by 3 <sup>rd</sup> year) compared to paired control plots, although marginally nonsignificant. Other invertebrate groups did not differ significantly in abundance or biomass. The manipulation did not exclude mice but only reduced abundance; low power may explain weak results. Not enough moth adults were found in either treatment to allow comparison.	Marion Island Southern Ocean	n1 = 5 n2 = 5	(Van Aarde et al., 2004)
<i>RN</i>	intertidal molluscs, small crabs, large shore crab <i>Leptograpsus variegatus</i>	Eradication (monitoring)	Possible suppression; unquantified, although numbers of these intertidal groups were 'considerably' greater after eradication. Terrestrial pitfall trapping was attempted, but was poorly controlled, with no baseline (pre-eradication) sample.	Motu-o-kura Island, NZ	n1 = 1	(Walls, 1998)
<i>R. spp</i>	Mahoenui Giant Weta <i>Deinacrida mahoenui</i>	Reintroduction (monitoring and comparison)	Suppression or local extinction (populations introduced to rat-free sites flourished; those at rat-present sites persisted 'in proportion to' the amount of rodent control, and those at sites with little or no rodent control went extinct)	North Island, Mahurangi Island and Motutapere Island, NZ	n1 = 6	(Watts and Thornburrow, 2009)
<i>RE</i>	Giant wetapunga <i>Deinacrida heteracantha</i>	Eradication (monitoring)	Suppression (capture rates have increased over 5 years, to twice the rate immediately following eradication. No baseline data)	Little Barrier Island, NZ	n1 = 1	Chris Green, Pers. Comm

RE	Most insect taxa >5mm in length, including ground weta <i>Hemidrus pallitarsus</i> , prowling spider species (Araneae: Miturgidae), various other spiders, beetles, and other arthropods including the giant centipede <i>Cormocephalus rubriceps</i>	Eradication (monitoring)	Suppression (capture rates of many taxa increased over the long term post-eradication; average increase in capture rates over 15 years since rat eradication are: ground Weta 1.7x, prowling spider >2.0x, all spiders over 5mm 1.6x, all beetles over 5mm 2.8x, all insects over 5mm pooled together 1.4x. Apparent species richness has also increased, with species such as a giant centipede <i>Cormocephalus rubriceps</i> only appearing in traps several years after rat eradication. No baseline data)	Tiritiri Matangi Island, NZ	n1 = 1	Chris Green, Pers. Comm and (Green, 2002)
MM	2 spider species ( <i>Uliodon</i> sp., Zoropsidae & <i>Meringa</i> sp., Synotaxidae) 2 moth larvae ( <i>Mallobathra</i> sp. & <i>Grypotheca</i> sp.) various beetles (3 Leiodidae: <i>Agaricalodes</i> sp., <i>Colon hirtale</i> & <i>Isocolon</i> sp.; 2 Carabidae: <i>Holcaspis oedictema</i> & <i>Zeopoecilus calcaratus</i> ; various others: Staphylinidae spp., <i>Carpophilus gaveni</i> (Nitidulidae) & <i>Melanophthalma variegata</i> (Corticariidae)	Eradication & natural experiment (comparison & monitoring)	Suppression; 8 beetle species increased in abundance after mouse eradication on Allports Is., one of which was absent from the baseline pre-eradication survey and 'common' afterwards. Although 5 beetle species also increased at the mainland control sites, the increases were 'much smaller' than on the island. The 2 spiders and 2 moths increased significantly after mouse eradication, but only 1 of these (the moth <i>Mallobathra</i> sp.) also increased on the mainland.	Allports Island & South Island NZ	n1 = 1 n2 = 2	Mike Fitzgerald pers. comm.; data also mentioned by (Ruscoe, 2001)
RN	1 giant endemic tenebrionid <i>Polposipes herculeanus</i>	Invasion (monitoring)	rapid suppression (80% decline after 5 years post-invasion). Thorsen et al also list a land snail and giant scorpion as being at 'high risk' from rat predation	Fregate Island, Seychelles	n1 = 1	Parr, 1999, cited in (Merton et al., 2002). Also see Thorsen et al. (2000)
RE	ground weta 1 beetle <i>Mimopeus opaculus</i>	Eradication (monitoring)	Probable suppression ('increases in capture frequency' of these species occurred after rat eradication)	Lady Alice Island, Chicken Islands, NZ	n1 = 1	Parrish & Towns, unpublished data cited in (Atkinson and Towns, 2002)
RN	endemic camel cricket <i>Parudenus falklandicus</i> Various beetle species including <i>Lissopteris</i> spp, <i>Caneorhinus biangulatus</i> , <i>Cylindrorhinus lemniscatus</i>	Natural experiment & eradication (comparison)	Suppression of beetles & crickets; lower abundance of large-bodied beetles and camel crickets on rat infested islands (n = 18) than rat-free islands (n = 13). Camel cricket abundance on rat-eradicated islands (n = 6) increases significantly with time elapsed since rat eradication.	Falkland Islands, UK Southern Ocean	n1 = 18+6 n2 = 13	St Clair et al., in prep
RE, RR, RN, MM	various Weta species ( <i>Deinacrida heteracantha</i> , <i>D. rugosa</i> , <i>D. carinata</i> , 2 unknown <i>Deinacrida</i> sp. <i>Hemidrus</i> sp.) 3 click-beetle species ( <i>Amychus</i> spp.) Campbell Island Ribbed Weevil <i>Heterexis seticostatus</i>	Various sources: Natural Experiment, Local Irruptions, Subfossil evidence	Suppression and/or local extinction (species absent or suppressed at sites/islands where rodents are present)	Various Islands, NZ	-	(Meads, 1990; Ramsay, 1978) *

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Weevils *Anagotus fairburni*, *A. turbotti*  
 Speargrass Weevil *Lyperobius huttoni*  
 Knobbled Weevil *Hadramphus stilbocarpae*  
 3 moth species (1 Noctuidae, 2  
 Oecophoridae)  
 Giant Centipede *Cormocephalus rubriceps*  
 Giant Pill Millipede *Procyliosoma*  
*tuberculata*  
 various unnamed beetle species including  
 stag beetles

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(Meads, 1990; Ramsay,  
 1978 (continued)) \*

\* A review by Ramsay (1978) and a book by Meads (1990) both contribute accounts of rodent impacts on dozens of New Zealand endemic invertebrates, although the sources of most data are not referenced; as there is likely to be considerable replication in their sources, I have pooled these data into a single row

## THE IMPACTS OF INVASIVE RODENTS

### *Responses*

Forty-five studies investigated population-level effects of invasive rodents on island invertebrates (Table 1). The majority of studies reported negative impacts of these rodents on island invertebrate populations, although four reported weak or negligible effects (King, 2007; Rufaut and Gibbs, 2003; Spurr, 1996; Van Aarde et al., 2004) and three reported a positive effect of rodent presence (Kurle et al., 2008; Rate, 2009; Sinclair et al., 2005). In some cases, a mixture of positive and negative effects are reported for different invertebrate taxa or size-classes (Craddock, 1997; Palmer and Pons, 1996 - see 'Indirect mechanisms' below). Suppression was the most commonly recorded effect of rodent presence, although twelve studies inferred local extinction of invertebrate populations of 16 species. The extreme declines of two restricted-range endemics following rodent invasion, the Lord Howe stick insect *Dryocelus australis* and the Frigate giant tenebrionid beetle *Polposipes herculeanus*, suggested that the species would have become entirely extinct in the wild without intervention. Several studies investigated effects on species richness or other measures of diversity; with most finding these indices lower when rodents were present (e.g. Bremner et al., 1984; Craddock, 1997; Towns et al., 2009) although the opposite effect also occurred (e.g. Sinclair et al., 2005).

### *Rodent species*

*Rattus exulans* was the best-represented, being the subject of nine studies; *M. musculus*, *R. norvegicus* and *R. rattus* were the subjects of seven, seven and five studies respectively, and the remainder investigated effects of two or more rodent species concurrently.

### *Location of studies*

The geographical locations of study sites exhibit two apparent patterns. Firstly, the majority (31/45 = 69%) of studies are from New Zealand and its offshore islands (Table 2). It is possible that New Zealand has an unusually high proportion of rodent-vulnerable invertebrate taxa (Meads, 1990), but the trend may also be explained by the unusually strong commitment to invasive species research in New Zealand, and to the fact that it lends itself historically and geographically to the conservation interventions that provide the framework for many studies. Australasia (principally New Zealand) has been the site of 54% of the world's 284 successful rodent eradications from islands up to 2006 (Howald et al., 2007), and in keeping with this geographical bias in interventions, a disproportionate number of studies which used rodent eradication to investigate impacts on invertebrates (11/13 = 85 %) were from New Zealand. Secondly, very few studies ( $n = 7$ , most from Hawai'i and the Seychelles, and one – albeit tenuous – from the Caribbean) were from the tropics, despite a clear tropical bias in the distribution of rodent-infested islands (Atkinson, 1985). Apart from those on New Zealand or its nearby offshore islands, most studies were from Southern Ocean Islands (sensu Chown et al., 2008) including the Falkland Islands, the Prince Edward Islands, the Kerguelen archipelago,

and the Antipodes archipelago. The median latitude (disregarding hemisphere) of non-NZ study sites in table 1 is 42°, while the median latitude of rat-infested islands according to published data is 19° (n = 120 islands or island groups; Atkinson, 1985), although the paucity of non-NZ studies ensures the difference is not statistically significant (Mann-Whitney test: U = 7679,  $P = 0.116$ ); when NZ sites are included in the analysis, the median latitude of rat-infested islands is 40° and the difference is highly significant (Mann-Whitney test: U = 8233,  $P < 0.001$ ). Any latitudinal bias may be due to differences in research effort, or to inherent vulnerability of invertebrate species at higher latitudes, for instance due to slower population growth rates or lower diversity in high-latitude invertebrate communities (Chown et al., 2004; Donlan and Wilcox, 2008). Work by Atkinson (1985) hints at another possibility; he notes bias away from tropical latitudes in the distribution of bird extinctions attributable to invasive rats, and speculates that prior exposure to native terrestrial predators (which are more common in the tropics) may be important in determining vulnerability to invasive rodents - an 'extinction filter' *sensu* Balmford (1996). Consistent with island invertebrates being subject to such extinction filters, only two reports of invasive rodent impacts on invertebrates come from island groups which may once have contained native rodent species (Palmer and Pons, 1996; Pascal et al., 2004), the majority coming from historically mammal-free New Zealand and the remainder from sites such as the South Atlantic Islands which have never contained endemic rodents.

Geographical location	<i>n</i> studies	proportion of total studies
Australasia - principally NZ	31	0.69
Pacific Ocean - principally Hawai'i	5	0.11
Southern Ocean	5	0.11
Indian Ocean	2	0.04
Mediterranean	1	0.02
Caribbean	1	0.02

**Table 2:** number of studies from different geographical regions

*Taxa affected* – the majority of studies which reported negative impacts concerned terrestrial arthropods, especially Coleoptera and Orthoptera. Impacts on terrestrial molluscs were the next most frequently reported. Only 7% of studies (or fewer) reported impacts on other invertebrate groups (Table 3).



Invertebrate group	<i>n</i> studies	proportion of studies
beetles	15	0.25
orthoptera	11	0.18
land snails	9	0.15
spiders & harvestmen	4	0.07
littoral molluscs & crustaceans	4	0.07
moths	3	0.05
myriapods	3	0.05
cockroaches	2	0.03
bugs	2	0.03
woodlice	2	0.03
micro-invertebrates	2	0.03
flatworms	1	0.02
stick insects	1	0.02
earwigs	1	0.02

**Table 3:** number of studies which report a negative impact of invasive rodents on different invertebrate taxa. Thus 25% of studies reported negative impacts on one or more beetle species, and so on. When effects on the same species were reported by two or more studies, only one was counted.

## MECHANISMS OF IMPACT

### *Direct effects*

Rodents may affect invertebrates directly (via predation) or indirectly via effects on the predators, competitors, prey, hosts or ecosystem engineers that regulate invertebrate abundance. Most studies do not attempt to distinguish direct from indirect mechanisms of impact, although inferences can be drawn from the patterns of impact across taxa. This is because rodents are predicted to prey selectively on particular types of invertebrate; in particular, those with a body size large enough to make them profitable food items (Pyke et al., 1977). The direct impact hypothesis predicts that negative effects will occur more frequently among rodent prey taxa than non-prey taxa. Given that large-bodied taxa form a tiny minority of invertebrates, they are indeed disproportionately well-represented in the studies collected here, with impacts on various Weta species, giant land snails and other exceptionally large taxa including a giant centipede and giant millipedes in New Zealand, a giant beetle in the Seychelles, and a giant stick insect on Lord Howe Island, Australia. Moreover, studies that measure differences in invertebrate abundance across a number of size-categories often find that larger-bodied invertebrates are negatively affected by invasive rodents more frequently

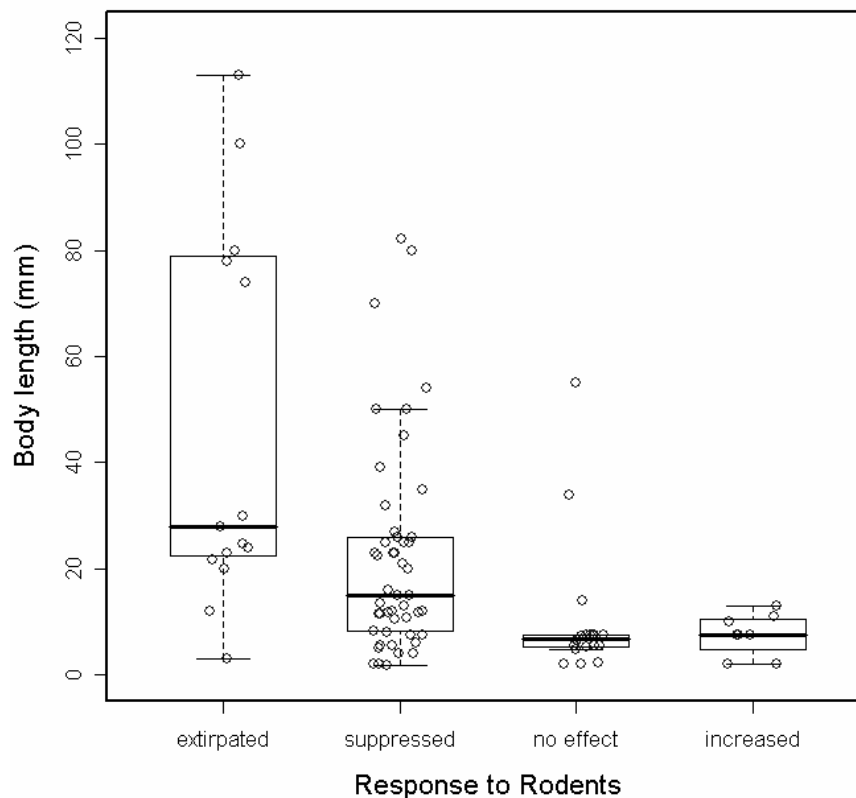
than smaller-bodied taxa (Bremner et al., 1984; Chown and Smith, 1993; Craddock, 1997; Chris Green, pers. comm.).

When data on named invertebrate taxa of known body size are collated from all studies reviewed here (on effects of *Rattus* species, mice and both in combination), it is apparent that invertebrate taxa that are thought to be extirpated (locally driven to extinction) by rodents tend to be larger-bodied than those that are merely suppressed, and that rodent-suppressed taxa have over twice the body length, on average, of those which are unaffected (Table 4, Figure 1). For this analysis, 'Extirpated' species are taken as those which were not found at rodent-infested sites, but which were recorded when rodents were absent (n = 16 species from 11 studies). There is no significant difference in the lengths of invertebrates that increase under rodent presence and those that are unaffected. The data are not numerous enough to investigate the effects of each rat species individually. However, when data for the three rat species are pooled they show that extirpated invertebrates are on average larger than suppressed ones, which are larger in turn than taxa which are unaffected or respond positively to rat presence. Data for mouse effects in isolation are sparse, but they suggest that suppressed invertebrates are larger-bodied on average than those which are unaffected or benefitted, although the difference is not statistically significant. Data from studies reporting effects of co-invasive rats and mice suggest that the relationship between invertebrate body size and vulnerability is less clear, with extirpated invertebrates being on average smaller-bodied than those which are simply suppressed (although the difference is not statistically significant, and sample sizes are small).

Overall, these results suggest that large invertebrate body size is a strong predictor of risk from invasive rodents, consistent with a direct mechanism of impact (predation) in many cases.

	Extirpated mm (n)	Comparison – extirpated vs suppressed	Suppressed mm (n)	Comparison – extirpated vs suppressed	No Effect mm (n)	Comparison – no effect vs increased	Increased mm (n)
<i>Rattus</i> spp. only	45.0 (9)	$\left\{ \begin{array}{l} P = 0.063 \\ U = 224.0 \end{array} \right\}$	19.0 (28)	$\left\{ \begin{array}{l} P = 0.002 \\ U = 600.0 \end{array} \right\}$	7.5 (8)	$\left\{ \begin{array}{l} P = 0.294 \\ U = 57.50 \end{array} \right\}$	7.5 (8)
<i>M.</i> <i>musculus</i> only	-	-	10.5 (14)	$\left\{ \begin{array}{l} P = 0.737 \\ U = 159.0 \end{array} \right\}$	6.4 (7)	-	4.8 (1)
rats+mice	23.0 (7)	$\left\{ \begin{array}{l} P = 0.935 \\ U = 44.5 \end{array} \right\}$	45.0 (5)	-	9.8 (2)	-	-
All studies	26.0 (16)	$\left\{ \begin{array}{l} P = 0.015 \\ U = 666.5 \end{array} \right\}$	15 (47)	$\left\{ \begin{array}{l} P = 0.003 \\ U = 1723 \end{array} \right\}$	7.2 (17)	$\left\{ \begin{array}{l} P = 0.808 \\ U = 222.5 \end{array} \right\}$	7.5 (9)

**Table 4:** Median body lengths (mm) of invertebrate taxa of known size, according to their population responses to the presence of invasive rats and mice (singly, in combination, and overall). Also presented are test statistics and P-values of Mann-Whitney U-tests of differences in body length between population-response categories.



**Figure 1:** relationship between body length (mm) and the response of island invertebrate species (or within-taxon size-classes) to rodent presence, derived from all reports in the literature for which body length data were available. Actual data (with jitter) shown in grey, box and whisker plots superimposed.

### *Indirect effects*

Here I use 'indirect effects' to refer to interactions between two species which require the presence of a third (intermediary) species, as opposed to direct pairwise interactions such as predation (Wootton, 1994). Indirect effects are frequently found to be important in population regulation, and are the subject of a growing genre of studies (Pace et al., 1999; Van Bael et al., 2003). The 'rampant trophic opportunism' (Paine, 1980) typical of the invasive rodents suggests a particularly wide range of potential indirect effects, due to direct impacts on groups occupying a diverse range of trophic levels and functional roles, from primary producers (plants) through primary consumers and mesopredators (such as other invertebrates) to top predators (often birds) and ecosystem engineers (including burrowing seabirds).

One of the first descriptions of a complex indirect effect involved rodents and invertebrates: Charles Darwin wrote that field mice *Apodemus sylvaticus* destroyed the combs and nests of bumble-bees *Bombus* sp., and that this particular bee alone pollinated red clover *Trifolium pratense*. Darwin speculated that a local increase in cat abundance "might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district!" (Darwin, 1859). Logic dictates that such indirect effects must occur frequently – for example, thousands of feather- and nest parasites must have been extirpated when rats drove their avian hosts to extinction (Ramsay, 1978; Steadman, 1997). It can be notoriously difficult to demonstrate indirect mechanisms of impact (White et al., 2006), but a number of studies, discussed below, indicate that invasive rodents can affect island invertebrates via indirect mechanisms.

### *Effects on invertebrates via their hosts*

A powerful mechanism of invertebrate extinction is thought to be the extinction or suppression of host organisms. When plant populations decline, there is clearly potential for parallel effects on symbiotic invertebrates including parasitoids, herbivores, frugivores and nectarivores (Dunn et al., 2009), and species for which plants provide essential habitat. A number of studies have demonstrated effects of introduced rodents (particularly *R. rattus* and *R. exulans*) on the distribution, germination or recruitment of plants (Campbell, 1978; Campbell and Atkinson, 2002; Phiri et al., 2009; Shaw et al., 2005; Wardle et al., 2007; Wilson et al., 2003), although only a few studies have addressed rodent impacts on invertebrate populations via effects on plants: the cushion plant *Azorella selago* is thought to be an important habitat for invertebrates on Marion Island, and its destruction by mice may affect invertebrate populations (Phiri et al., 2009); regeneration of Karo plants *Pittosporum crassifolium* is strongly inhibited by *R. exulans*, and when this plant species recovered on New Zealand islands following eradication of rabbits and *R. exulans*, populations of the endemic scale insect *Coelostomidia zealandica* also recovered (Campbell and Atkinson, 2002; Towns, 2002). Finally, the local extinction of the large weevil *Hadramphus stilborcarpae* occurred at the same time as the severe reduction of its host plant *Stilbocarpa lyelli* by *R. rattus* shortly after they invaded Big South Cape Island in New

Zealand (Kuschel and Worthy, 1996). In each of the latter examples it was not possible to demonstrate a rodent-plant-invertebrate pathway due to potentially confounding variables, although it seems likely that such a mechanism at least contributed to the observed impacts.

#### *Effects on invertebrates via their predators*

Impacts of introduced rodents on many native predator populations are known, including birds, mammals and reptiles as well as predacious invertebrates (Towns et al., 2006). Given these impacts, it is perhaps surprising that there are relatively few recorded examples of subsequent prey release. Perhaps the best example is from the Aleutian islands, where invasive rats have caused severe local reductions in the density of shorebirds such as oystercatchers, and populations of invertebrates (on which these shorebirds prey) in the intertidal zone have increased substantially relative to those around rat-free islands (Kurle et al., 2008). Such trophic cascades are currently receiving considerable attention, and more examples of rodent-mediated mesopredator suppression and prey release may emerge in the coming years. Trophic cascades *within* invertebrate communities are seldom studied, but given that taxa with an important predatory role such as carabid beetles may be particularly susceptible to rodent predation (Ernsting et al., 1995; McGuinness, 2007; Parmenter and Macmahon, 1988) it seems likely that rodent-initiated trophic cascades are a common but under-recorded post-invasion event. It may not be coincidental that rodent-caused suppression of large-bodied (predacious) invertebrate taxa is sometimes accompanied by an increase in smaller-bodied (prey) groups (e.g. Craddock, 1997).

#### *Effects on invertebrates via their competitors*

When a species is removed from a community, the vacated ecological space can benefit its competitors (Schoener, 1983). Introduced rodents clearly have population-level impacts on various species, and competitive release of their competitors might be expected. A prerequisite for this effect is a differential impact of rodents on species within competing pairs; in nature, competing species are likely to be vulnerable to the same predators and thus competitive release will frequently not arise. Exceptions may occur when one competitor has superior anti-predator adaptations, an advantage that invasive invertebrates may have over native species (Blumstein and Daniel, 2005; Lovei and Sunderland, 1996); this is thus a candidate mechanism for rodent-mediated facilitation (sensu Simberloff and Van Holle, 1999) of invertebrate invasions. This is a possible explanation (albeit one of several) for Palmer and Pons' (1996) finding from 51 Balearic Islets, in which five endemic tenebrionid beetles were significantly less likely to occur on rat-infested islands, while two non-endemic species (with well-developed chemical antipredator defenses) were *more* likely to occur on rat-infested than rat-free islands.

#### *Effects on invertebrates via ecosystem engineers*

A series of studies from New Zealand have demonstrated cascading effects of invasive rats on invertebrates; predation by introduced rats severely reduced the density of burrowing seabirds

compared to that on uninvaded islands, causing a marked reduction in the marine nutrient subsidy (Fukami et al., 2006), increased tree recruitment, atmospheric carbon sequestration and plant biomass (Wardle et al., 2007), reduced nitrogen content in the soil and some plant species (Mulder et al., 2008; Wardle et al., 2009), a reduced rate of litter decomposition and nitrogen release (Wardle et al., 2009), and reduced abundance of many below- and above-ground invertebrate groups (including minute land snails, springtails, rotifers, centipedes, ants, moths, amphipods and various vermiform taxa) attributable to the effects of rat-mediated seabird declines on soil characteristics (Fukami et al., 2006; Towns et al., 2009). Reductions of breeding seabird density, and concomitant reductions of marine nutrient inputs, are common consequences of rodent invasion of 'seabird' islands (Towns et al., 2006) and although nutrient and plant-related effects on invertebrate communities may commonly occur they are seldom investigated.

#### *Evolutionary impact*

Island species often lack adaptations to non-native predators, and invasive rodents have clear potential to cause rapid evolutionary change in these species. Insular invertebrates often have remarkable morphologies such as gigantism, which likely result in part from a rodent-free evolutionary history (Gibbs, 2009; Meads, 1990). Novel predators such as rodents are likely to impose strong selection on heritable traits which affect the vulnerability of native prey, which may include body size, anti-predator defences, fecundity and age-at-maturity and other morphological and life-history traits (Fisk et al., 2007; Strauss et al., 2006). Evolution in response to such pressures will not only alter native gene pools, but changes to life-histories also have the potential to affect population dynamics and, in turn, ecosystem properties (Pelletier et al., 2009). Rapid evolutionary responses among island invertebrates are likely to occur following rodent introduction for a combination of reasons: firstly, the widespread ability of invertebrate prey to co-exist with rodents at reduced densities and the typically short generation time of invertebrates are both conditions necessary for rapid evolutionary responses; secondly, because insular invertebrate species will already possess adaptations to native (usually avian or reptilian) predators there is likely to be considerable existing variation in life-history and anti-predator traits upon which selection can act; and finally, the selection pressures imposed on these traits by efficient and functionally alien predators such as rodents are likely to be intense. Despite this, I am aware of no convincing demonstrations of rapid evolutionary responses following rodent invasion of islands, although one study records that three invertebrate species sampled from rat-infested islands showed much greater predator-escape responses than the same species from rat-free sites (Bremner et al., 1989), and Meads (1990) mentions two New Zealand giant myriapod species and a stag beetle *Dorcus helmesii* which only reach their largest sizes on rodent-free islands; this may be due to selection of the largest individuals by rodents, or (more likely) to generally increased predation pressure that shortens average and maximum lifespans and prevents recruitment to old (large) size-classes. Either way, the potential for directional selection and evolutionary change is clear.

## STUDY DESIGNS AND LIMITATIONS

Most studies relied on natural or experimental variation in rodent presence or abundance across sites, time periods or both. Response variables included presence/absence of focal invertebrate taxa or size-classes determined by trapping or searching, and indices of relative abundance or species richness estimated using pitfall captures, tracking tunnels or capture/recapture methodologies. A second study type used quantification of rodent diet together with estimates of invertebrate demography to infer a population-level impact (also see Navarrete and Castilla, 1993; Rowe-rowe et al., 1989). Other studies used predation sign (characteristic shell breakage in snails) to correlate invertebrate population declines with rodent predation levels (Hadfield et al., 1993; Hadfield and Saufler, 2009; Meyer and Shiels, 2009). This forensic approach has also proved valuable in studies of prehistoric impact, with shell-breakage patterns implicating *R. exulans* in the the extinction of several NZ endemic land snail populations (Brook, 1999; Brook and McArdle, 1999). A distinct and powerful study type uses the deliberate introduction of putatively vulnerable invertebrate populations to sites of varying rodent status – persistence time and population trajectories can then be used to infer impact (Watts and Thornburrow, 2009).

Varying levels of control and replication were used in different study types. All studies of rodent invasion were unreplicated, reflecting the accidental nature of the variation and the opportunistic nature of the studies. More striking is the finding that the majority ( $7/13 = 54\%$ ) of studies which used deliberate rodent eradication as the source of variation also lacked any replication or spatial control, relying on repeated measurement of invertebrate abundance at a single manipulated site. Furthermore, many of these time-series studies lacked baseline (pre-manipulation) data, or relied on a single pre-manipulation sampling event (e.g. Green, 2002).

Questions of replication and control aside, the choice of method has important implications for the results. It is interesting to note that of the four studies that found no population-level treatment effect, three used methods which merely reduced rodent abundance rather than removing them completely, which suggests that even low rodent densities may be enough to suppress the recovery of invertebrate populations (the fourth found population impacts were probably mitigated by changes in anti-predator behaviour when rats were present - Rufaut and Gibbs, 2003). Furthermore, a key feature of manipulative designs (eradication, control and exclosure) is that they can only test responses to rodent removal among the subset of species which were able to persist after the initial rodent invasion – in other words, the approach can not detect responses among species which are locally driven to extinction by rodents unless there is rapid recolonisation from nearby healthy populations (Townes, 2009). Designs that record the response of invertebrate populations to manipulation of rodent presence or abundance are thus inherently subject to Type 2 error. On the other hand, natural experiments *can* be used to infer local extinction of invertebrate populations, but care must be taken to account for confounding

variables, such as accessibility or the level of anthropogenic disturbance, which might simultaneously favour rodent presence and negative effects on invertebrate populations. Such confounds raise the probability of Type 1 error in natural experiments.

Such problems may be satisfactorily addressed by the use of combinatorial designs, which consider two or more mutually supporting lines of evidence. Such combinations may include the incorporation of manipulated (rodent-eradicated) sites into natural experiments, or other methods (discussed above) such as subfossil chronology, dietary studies and invertebrate reintroduction.

## CONCLUSIONS AND FUTURE DIRECTIONS

Taken together, the studies collected here suggest that impacts of invasive rodents on island invertebrates are globally widespread, although they have been investigated largely in New Zealand. These impacts involve direct and indirect mechanisms, and are phylogenetically diverse, with effects on several invertebrate phyla documented for each of the four invasive rodent species. In several cases invertebrate populations have apparently been driven to extinction by invasive rodents, but the most commonly recorded impact is population suppression. Negatively affected invertebrates tend to be larger-bodied than those which are unaffected by rodents, a trend which may be driven by rodent dietary preferences and/or life-history correlates of large body size that confer vulnerability (at the population level) to increased predation. Further research is urgently needed to investigate, for each rodent in turn, the distribution, severity, mechanisms and population and ecosystem consequences of these rodent-invertebrate interactions. I also hope that opportunistic, incidental and small-scale studies which make up the bulk of the literature reviewed here, and which are often conducted alongside or as part of conservation management programmes, will in future be supplemented by more dedicated research projects which are not limited by the need to divide valuable resources between research and conservation action. Some areas in which this effort could profitably be focussed are outlined below.

### *Differences and interactions between rodent species*

The effects of the three *Rattus* species and *Mus musculus* on prey populations may or may not be broadly equivalent (Angel et al., 2009), and largely for reasons of data availability I have not attempted to distinguish between their impacts in this review. However, these rodent species have different distributions and foraging ecologies, which may lead to differences in their impacts on prey species including invertebrates (Amarasekare, 1994; Atkinson, 1985; Harper, 2006). There is thus a clear need to know about their relative impacts when prioritising eradication, or when planning conservation management of sites at which two or more (potentially interacting) invasive rodent species are present (Clout and Russell, 2007). Further research into the impacts and demographic interactions of different invasive rodents (and other common invasives including stoats, cats and foxes) would also be of considerable value,



allowing the consequences of step-wise or partial eradications of alien communities to be modelled in advance, and 'surprise effects' to be avoided (Caut et al., 2009).

#### *Indirect effects*

It is clear that indirect effects of rodents on invertebrates are often mediated by direct impacts on keystone vertebrates (Kurle et al., 2008; Towns et al., 2009). However, this review would not be complete without encouraging greater consideration of the potential *consequences* of rodent-invertebrate interactions for other ecosystem components. Although invertebrates are vital for ecosystem functioning, relatively few studies have yet investigated the knock-on effects of the suppression of invertebrate species on other ecosystem properties such as native predator guilds, soil processes, invertebrate community structure and resilience to further invasions (Huyser et al., 2000; Lawrence and Samways, 2003; Pisanu et al., 2005; Simberloff and Van Holle, 1999). Effects such as these may be important mechanisms of change in invaded ecosystems, and are pertinent both to conservation biology and to basic research in ecology and biogeography.

#### *Towards a predictive framework of vulnerability*

Among vertebrate taxa, considerable effort has gone into identifying the phenotypic and phylogenetic correlates of extinction risk, ostensibly to generate predictive frameworks to inform conservation management (Fisher and Owens, 2004; Reynolds et al., 2005). However, the question of correlates of extinction risk in invertebrates has seldom been addressed (Krushelnicky & Gillespie, 2010). I suggest that such studies, which can lead to the identification of particularly vulnerable guilds or taxa, may be of considerable use in the prioritisation of conservation interventions such as rodent eradications. A clear correlate of vulnerability to invasive rodents highlighted in this review is large body size, and a knowledge of threshold body sizes – above which the risk from a given invasive rodent species is substantially increased – may prove to be a valuable tool for conservation managers. In addition to large body size, other risk factors have been proposed – flightlessness, ground-dwelling habits, strong odours, and a lack of anti-predator adaptations such as escape responses and distasteful compounds may all increase vulnerability (Gibbs, 2009), and to this list of candidate traits we can add life-history traits such as delayed reproductive maturity and low reproductive output which often confer vulnerability at the population level (Fisher and Owens, 2004). Studies that record variation in such phenotypic traits across a spectrum of rodent-affected and -unaffected invertebrate species may prove invaluable in constructing a predictive framework of risk.

#### *Evolutionary responses to rodent invasion*

As discussed in the 'Evolutionary impact' section above, the suppression of invertebrate populations by invasive rodents provides the conditions necessary for rapid evolutionary change. To date, there has been little investigation of evolutionary responses of native species

to invasives in any system (Strauss et al., 2006). Given that rapid evolutionary change can reduce ecological effect sizes and facilitate persistence of native species in the presence of invasives (Pelletier et al., 2009), the phenomenon is likely to structure disturbed communities and merits further attention. Furthermore, rapid directional evolution may also represent a mechanism for the cryptic loss of biodiversity, reducing genetic variance (Roff, 1997) and eroding the very characteristics that make many island endemics 'special' or phenotypically distinct from their continental relatives – in the case of New Zealand's invertebrates, such characteristics include gigantism (Meads, 1990). In invertebrates, evolved differences are relatively easy to detect using common-garden experiments, in which phenotypic assays are conducted on cultured populations originating from different sites (e.g. those with and without invasive rodents), and I suggest that such studies may provide fascinating insights into a cryptic and neglected aspect of species invasions.

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## **Chapter 8: CONCLUSIONS AND FUTURE DIRECTIONS**

James J. H. St Clair

## OVERVIEW

In this thesis, I have presented the results of observational studies of bird breeding behaviours and life-histories, and of natural-experimental studies (and a literature review) of the effects of mammalian predators on island populations. Notable findings are:

- two closely-related and sympatric waders in the Falkland Islands (the Two-banded Plover *Charadrius falklandicus* and Rufous-chested Dotterel *Charadrius modestus*) showed opposite diel sex-roles in incubation, with males incubating during the night in the former species and during the day in the latter.
- the Two-banded Plovers on Sea Lion Island had a high estimated rate of annual adult survival (92%), and a very low rate of nest success (13%). In the absence of mammalian predators, nest predations occurred exclusively during the day.
- comparison of the anti-predator behaviour (flushing distances) expressed by Two-banded Plovers at different sites in response to an approaching human showed that flushing distances are substantially higher when invasive mammalian predators (cats) are present, and when nests are located at sites with relatively little human activity.
- an endemic insect, the Falkland Camel Cricket, had a higher estimated abundance in certain habitat types (specifically Tussac Grass *Poa flabellata*) than others, and was also estimated to be much more abundant when rats (*Rattus sp.*) were absent (both naturally and due to deliberate eradication) than when they were present.
- a review of the effects of invasive rodents on island invertebrates showed that population suppression in the presence of rodents is not limited to the Falkland Camel Cricket and may be a common post-invasion event, and that such a response is more likely to occur amongst large-bodied invertebrates than smaller-bodied species.

As several of these studies are only tenuously relevant to each other, if at all, I cannot boast that the thesis makes a substantial gain in any single field of research; rather it advances several different fields by modest increments. Below, I discuss some of the implications of these studies, and a few potentially profitable directions for future research.

## DISCUSSION AND FUTURE DIRECTIONS

### Knowledge gaps

In the introduction to this thesis, I identified knowledge gaps and bias in the distribution of knowledge within avian datasets as arguments for carrying out descriptive studies of bird life-histories and breeding systems. Some such knowledge gaps about the plovers of the Falkland Islands have now been eliminated, and the thesis thus helps (albeit in a small way) to redress the relative lack of knowledge of South American birds and of under-represented data types

such as survival rates. I suggest that a quantitative assessment of knowledge gaps in avian datasets would prove valuable in the future, both for prioritising descriptive projects, and for determining the possible effects of missing value biases on the results of comparative analyses. A possible bias in the representation of avian life-histories in comparative datasets stems from the combination of a geographical bias (away from tropical and southern temperate regions) in the distribution of available life-history data (e.g. Thomas et al., 2003), and an ecogeographical bias in the distribution of life-histories, with apparently consistent differences in bird life-histories between populations with northern temperate and tropical or southern temperate distributions (Martin et al., 2000). The possibility thus arises that the data used in comparative analyses of life-history evolution may be both non-random and unrepresentative of the global distribution of bird life-histories in nature. Until biases in the available data are known and their effects assessed, we cannot know whether this is an academic issue of limited impact, or one that might significantly affect our understanding of subjects including demography, conservation and the evolution of life-histories in birds.

### **Behaviour patterns while incubating**

In chapters two and three I showed that two sympatric, congeneric plover species show opposite diel sex-roles in incubation, and chapter five demonstrates between-population differences in the expression of anti-predator behaviour in the Two-banded Plover. Although these studies seem relatively unrelated, an interesting common thread concerns the costs and benefits of different behaviour patterns during incubation. In the discussions of diel sex-roles I echo earlier suggestions that the costs and benefits of daytime incubation may differ from those of nighttime incubation, while in the anti-predator behaviour study I assume, like many previous workers, that flushing from the nest in response to perceived threats carries some costs in addition to the benefit of potentially reducing the risk of nest predation (Caro, 2005; Skutch, 1957). However, although several studies have measured or inferred time, opportunity, energy and mortality costs of incubation in other wader species (e.g. Amat and Masero, 2004; Cresswell et al., 2003; Tulp et al., 2009), we still lack a sound understanding of how variation in incubation behaviour affects the sign and magnitudes of costs and benefits for (separately) parents and their eggs, how these costs and benefits are modulated by the environment, and how they ultimately affect fitness. There is plenty of scope for empirical measurement of these costs and benefits in nature. Such data would allow a more meaningful estimation of the division of parental effort, which is of key importance for improving our understanding of the evolution and maintenance of parental care strategies and other reproductive strategies such as polygamy and sex-role reversal (Alonzo, 2009). The same data could also contribute to the development of a theoretical framework that addresses optimal behaviour among incubating birds during predator approaches, similar to that which has already proved useful in explaining the behaviour and distribution of foraging animals (Lima and Dill, 1990). Such a framework is conspicuously lacking for incubating birds (Lima, 2009), but would be relevant to studies of

variation in incubation behaviour, adult and juvenile mortality (and hence demography), breeding distributions, and the effects of non-lethal stimuli including human disturbance.

### **Effects of mammalian predators**

The natural experiment studies of the effects of mammalian predators (chapters five and six) were each conducted over a single field season, and there is a great deal of scope to test their assumptions and improve and consolidate their findings. Our understanding of anti-predator behaviour in Two-banded Plovers would benefit from a more detailed investigation of the actual interactions of potential mammalian and avian predators and breeding plovers, and from experiments to confirm that the pattern of between-site variation in anti-predator behaviour expressed in response to human stimuli is also expressed in response to genuine live or model predators (e.g. Curio et al., 1983). It may also be profitable to incorporate anti-predator behaviours besides flushing into such studies, as after flushing from the eggs, plovers frequently return to the vicinity of the stimulus to perform distraction displays, one of a fascinating repertoire of wader anti-predator behaviours that were not considered in the presented study (Caro, 2005). Similarly, there is plenty of scope to improve our understanding of the interaction between invasive rodents and Falkland Camel Crickets. Studies of Camel Cricket life-histories at sites with and without rats combined with analysis of rat diets would tell us about the mechanism of impact, and studies of the ecological function of Camel Crickets would cast light on some of the possible indirect effects of rodent invasion in the Falkland Islands.

In general, the scope for further studies of the effects of mammalian predators in the Falkland Islands is immense. For example, with the exception of a few studies of the impact of ship rats (*Rattus rattus*) on the seabirds of New Island (Quillfeldt et al., 2008) I am aware of no empirical studies of the effects of invasive mammals on potentially vulnerable seabird populations in the Falkland Islands, but such studies may be of considerable value to the conservation of several potentially vulnerable breeding seabird species (Croxall et al., 1984; Hilton and Cuthbert, 2010).

### **The Falkland Islands as a study site**

One of the most important outcomes of this PhD may be the demonstration that the Falkland Islands form a viable study system of potentially immense value as a natural experiment. The great number of accessible islands, which contain a spectrum of native species and a range of non-native species including plants, insects, mammalian predators and herbivores, makes a versatile system for both inferring pairwise interactions such as those between mammalian predators and native species (e.g. chapters five and six) and potentially for investigating more complex interactions such as trophic cascades, mesopredator release and invasional facilitation. With respect to the effects of mammalian predators, this utility is greatly increased by the conservation actions that have recently gathered pace in the Falklands – rat eradications have so far been attempted on thirty of the Falkland Islands (Hilton and Cuthbert, 2010). Any

future inter-island experiments need not be restricted to the effects of invasive predators, as herbivores including cattle, sheep and rabbits have also been introduced to many islands. The natural experimental framework that applies so well to predator-prey interactions would serve just as well to investigate the consequences of herbivore introduction for the vegetation and animals that depend on it, and for ecological properties such as nutrient cycling and soil formation.

### **Insular selective landscapes**

The final three data chapters are of value because they address little-known aspects of a ubiquitous problem, the introduction of novel predators to islands. These chapters all suggest that in addition to the well-known rapid extinctions of charismatic vertebrates, novel predators can produce altogether more subtle effects that would most likely escape the notice of a casual observer. The fact that introduced mammalian predators may alter the anti-predator behaviour expressed by nesting plovers in response to non-lethal disturbance, or powerfully suppress populations of certain insects, hints that selective landscapes in invaded systems may be altered in myriad ways that are both predictable and unpredictable. The changes to selective landscapes that follow predator introduction – or other anthropogenic changes – merit future research for a number of reasons. Firstly, the differences in selective landscapes between islands and continents may serve to explain why insular organisms are often so different from their continental relatives; a suite of exceptional behavioural, morphological and life-history changes often evolve following isolation on islands, but their causes are more often speculated on than empirically investigated (Blondel, 2000; MacArthur and Wilson, 1967). Secondly, some of these evolutionary changes may explain the massively elevated risk of extinction faced by island organisms, and an understanding of these intrinsic components of vulnerability (and their importance relative to extrinsic components such as small population sizes) may help conservationists to identify and manage vulnerable populations. Finally, the altered selection pressures that arise from novel interactions within invaded communities, and the ability of both invasive and native species to respond to them, offers an exciting opportunity to study evolution in action (Blackburn, 2008; Sax et al., 2007). An understanding of these questions might also offer a glimpse of what invaded systems will look like in the evolutionary future: which species will be long gone, which will still be there, and how they will differ from their ancestral forms.

### **Future output**

A considerable amount of information has been collected during my studies which has not been included in the thesis due to time limitations, but which will be prepared for publication. Data from the field include life-history, behavioural and ecological observations from both Falkland Islands plover species, capture data for additional invertebrate groups (such as beetles) from the pitfall surveys on islands of different rat status, and bird surveys from each of the same islands. Passerine birds sampled in 2009 will provide the basis of a genetic and phenotypic

comparison of the populations of the Falkland Islands and continental South America (L. Campagna, J. St Clair et al., in prep.). Based on large-scale (global) datasets, I have also initiated a collaboration to investigate, using comparative analyses, the effects of climatic variance (rather than mean values) on annual adult survival and associated life-history traits among migrant and non-migrant bird species (G. Garcia-Pena, J. St Clair et al, in prep.).

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